


Ex libris
UNIVERSITATIS
ALBERTAENSIS





Digitized by the Internet Archive
in 2023 with funding from
University of Alberta Library

<https://archive.org/details/Douglas1973>

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR ..GEORGE WAYNE DOUGLAS.....
TITLE OF THESIS ..Alpine Plant Communities of the North
.....
.....Cascades Range, Washington and.....
.....British Columbia.....
DEGREE FOR WHICH THESIS WAS PRESENTED ..Ph.D.....
YEAR THIS DEGREE GRANTED ..1973.....

Permission is hereby granted to THE UNIVERSITY OF
ALBERTA LIBRARY to reproduce single copies of this
thesis and to lend or sell such copies for private,
scholarly or scientific research purposes only.

The author reserves other publication rights, and
neither the thesis nor extensive extracts from it may
be printed or otherwise reproduced without the author's
written permission.

THE UNIVERSITY OF ALBERTA

ALPINE PLANT COMMUNITIES OF THE NORTH CASCADES RANGE,
WASHINGTON AND BRITISH COLUMBIA

by



GEORGE WAYNE DOUGLAS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1973

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Alpine plant communities of the North Cascades Range, Washington and British Columbia" submitted by George W. Douglas in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Ecology.

ABSTRACT

Twenty-three major community types were described from 128 stands in the alpine zone of the North Cascades Range. These included six snowbed types (*Saxifraga tolmiei*-*Luzula wahlenbergii*, *Eriogonum pyrolaeifolium*-*Luzula wahlenbergii*, *Carex nigricans*, *Antennaria lanata*, *Carex breweri*, and *Carex capitata*), two lush herb types (*Lupinus latifolius* and *Festuca viridula*), eight dwarf shrub types (*Cassiope mertensiana*, *Phyllodoce empetriformis*, *Phyllodoce glanduliflora*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, *Salix reticulata*, *Salix cascadiensis*, and *Dryas octopetala*), two dry grass types (*Danthonia intermedia* and *Calamagrostis purpurascens*), and five dry sedge types (*Carex spectabilis*, *Carex phaeocephala*, *Carex scirpoidea* var. *pseudoscirpoidea*, *Carex nardina*, and *Kobresia myosuroides*). Thirty-nine blockfield stands and 42 krummholz stands were also examined. Most of the major community types are closely related to those in the Rocky Mountains, southern Alaska and the southern Yukon.

Soils in the region include Entisols, Inceptisols, and Spodosols. Physical properties are quite similar in most soils. Organic matter, total cation exchange capacity, and pH generally decrease from west to east while exchangeable cations and nutrient levels are low throughout the region.

Species richness, general diversity, and equitability were low in the mildest habitats. Estimates of these parameters increased with an increase in environmental rigor and habitat heterogeneity until physical factors once again rendered the habitat homogeneous. At this point species richness and general diversity again declined.

A fellfield-dry grass-lush herb environmental gradient was examined on Grouse Ridge, Mt. Baker. High soil temperature and low soil moisture regimes were typical of the ridgetop fellfield. During drought periods, on the vegetated portion of the slope, soil temperatures decreased and soil moisture stress increased with distance downslope; a reflection of increased plant cover and greater evapotranspiration towards the base of the slope. Species exhibiting vigorous growth and high leaf water potential at the base of the slope had reduced vigor and much lower leaf water potential upslope. Phenological patterns were closely related to date of snowmelt and early season temperature regimes along the gradient.

ACKNOWLEDGEMENTS

The advice and assistance of Dr. L. C. Bliss, throughout the course of this study is gratefully acknowledged. I am indebted to Drs. G. H. La Roi, J. M. Mayo, W. W. Petta-piece, and D. H. Vitt for providing suggestions and critical review of the manuscript.

The aid of Dr. S. Pawluk is also appreciated. Dr. J. G. Bockheim assisted in describing several of the soil profiles. Summer laboratory facilities were provided by Dr. R. W. Fonda. Dr. T. M. Ballard provided specifications for construction of the bridge-meter. The computer program for the plant diversity indices was written by Mrs. D. Schwartz.

Special thanks are due to my wife, Gloria. Her patience and untiring aid during the many long days in the field and the multitude of hours in the office and laboratory made the study a pleasure.

Thanks are due to the following taxonomists who kindly spent time identifying or verifying difficult taxa: C. D. Bird, A. Cronquist, G. G. Douglas, C. Feddema, F. J. Hermann, C. L. Hitchcock, N. H. Holmgren, G. A. Mulligan, M. Ostafichuk, W. L. Peterson, R. Stotler, R. J. Taylor, and D. H. Vitt.

The cooperation and logistical support provided by the staff of North Cascades National Park is also appreciated. This study was supported by National Research Council Grant NRC A-4879 Bliss.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS	v
INTRODUCTION	1
STUDY AREA	3
Location	3
Geology and Geomorphology	5
Climate	9
METHODS	9
Vegetation	9
Soils	15
Climate	15
Phenology	17
Physiology	17
RESULTS	18
Regional vegetation	18
Snowbed community types	18
Lush herb community types	35
Dwarf Shrub community types	41
Dry grass community types	47
Dry sedge community types	52
Blockfields	55
Krummholz stands	62
Plant diversity	67
Soils	68
Morphology	68
Physical and chemical properties	77
Mesoclimate	81
Precipitation	81
Temperature	81
Atmospheric moisture	84
Solar radiation	84
Wind	84
Environmental Gradient	85
Vegetation	85
Plant diversity	93
Soils	94

TABLE OF CONTENTS CONTINUED

	<u>Page</u>
Mesoclimate	98
Microclimate	102
Physiology	110
Phenology	112
DISCUSSION	116
Community Pattern	116
Community-soil relationships	121
Alpine plant diversity patterns	122
Response of species to an environmental gradient	124
Distribution of major alpine community types in Western North America	127
SUMMARY	133
LITERATURE CITED	137

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Mean prominence values of species in the major community types of the alpine zone.	23
2	Mean prominence values and constancy of the major plant species in blockfield stands of four areas in the North Cascades.	60
3	Mean prominence values of plant species in four krummholz types in three regions (west, central, and east) of the North Cascades Range.	63
4	Physical and chemical properties from 12 soil profiles in the North Cascades.	78
5	Environmental data for five weather stations in the North Cascades Range.	83
6	Mean prominence values for all species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.	87
7	Physical and chemical properties from seven soil profiles along an alpine environmental gradient, Grouse Ridge, Mt. Baker, Washington.	99
8	Seasonal leaf water potential (bars) of 10 plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971.	111

LIST OF TABLES CONTINUED

Table

Page

9	Numbers of alpine plant communities associated with the three vegetation belts or bands found at upper elevations in the North Cascades.	129
---	---	-----

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Map of the study sites in the North Cascades Range of Wahington and British Columbia	4
2	Temperature-precipitation climograph of mean monthly values at Diablo (western North Cascades) and Winthrop (eastern North Cascades) weather stations (data from U.S. Weather Bureau, no dates).	10
3	Ordination of 128 stands in the alpine zone of the North Cascades.	20
4	Distribution of snowbed and lush herb community types in the North Cascade Range.	22
5	An <i>Antennaria lanata</i> community in a slight depression at 2180 m on Crater Mountain, Washington. The <i>Cassiope mertensiana</i> community occurs on the adjacent slopes.	33
6	A <i>Carex capitata</i> community at 2380 m on Arnold Peak, Washington. The <i>Carex scirpoidea</i> var. <i>pseudoscirpoidea</i> community cover the extensive slopes in the background.	37
7	A <i>Lupinus latifolius</i> community at 1980 m on Glacier Peak, Washington. The <i>Empetrum nigrum</i> occurs on the adjacent	

LIST OF FIGURES CONTINUED

<u>Figure</u>		<u>Page</u>
	upper slopes.	40
8	Distribution of dwarf shrub community types in the North Cascades Range.	42
9	A <i>Dryas octopetala</i> community at 2410 m on Windy Peak, Washington.	49
10	Distribution of dry sedge and dry grass community types in the North Cascades Range.	50
11	A <i>Kobresia myosuroides</i> community at 2400 m on Arnold Peak, Washington.	57
12	Means and standard deviations (vertical lines) of species richness, general diversity, and equitability in relation to environmental rigor.	70
13	Vegetation-soil relationships along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.	86
14	Distribution and abundance of major plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.	90
15	Vegetation along an environmental gradient at 1900 m on Grouse Ridge, Washington.	92
16	Relationship between species richness (S), general diversity (H), and equitability (E) along an environmental gradient on Grouse	

LIST OF FIGURES CONTINUED

<u>Figure</u>		<u>Page</u>
	Ridge, Mt. Baker, Washington.	95
17	Seasonal variation in temperature, VPD, solar radiation, and precipitation at the Grouse Ridge weather station during 1970, 1971, and 1972.	101
18	Seasonal variations in soil and air temperature profiles at various heights (cm) and depths (cm) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971.	104
19	Seasonal variations in soil and air temperature profiles at various heights (cm) and depths (cm) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1972.	106
20	Soil moisture regimes at four stations along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1970, 1971, and 1972.	109
21	Phenological patterns for 12 plant species on Grouse Ridge, Mt. Baker, Washington during 1971 (upper bar) and 1972 (lower bar).	115

INTRODUCTION

Ecologists have focused their attention on alpine environments for many years. These regions with extreme environments provide an excellent opportunity for the study of species and community patterns. These patterns are usually accentuated in alpine regions because of topographic diversity and often change abruptly due to rapid shifts in environmental gradients. Several other advantages of alpine vegetation studies are the relatively small flora, the dwarfed stature of the plants, and the reduced community structure (Bliss, 1969).

High mountain vegetation in the Northwest Pacific Coast region has received attention only recently. The rugged physiography of the region, its inaccessibility, and a frequently unfavorable summer climate have all contributed to this lack of ecological study. Studies have been completed in the Olympic Mountains of Washington (Bliss, 1969; Fonda and Bliss, 1969; Kuramoto and Bliss, 1970), the western North Cascades of Washington (Douglas, 1972), the southern Coast Range of British Columbia (Archer, 1963; Brooke *et al.*, 1970), and in the eastern North Cascades of British Columbia (McLean, 1970). Localized or more general accounts of the vegetation or flora have been provided for the Olympic Mountains (Peterson, 1971), the western North Cascades of Washington (Franklin and Dyrness, 1969;

Kruckeberg, 1969; Douglas, 1971; Douglas and Ballard, 1971; Lowery, 1972), the eastern North Cascades of Washington (Arno and Habeck, 1972), the southern Coast Range of British Columbia (Brink, 1959), and the Interior Plateau region of south-central British Columbia (Eady, 1971). A general phytogeographic survey of northwestern North America has been presented by Schofield (1969).

This study examines the plant communities of the alpine zone in the North Cascades of Washington and British Columbia. The objectives of the study were to 1) obtain quantitative and qualitative data on the composition, structure, pattern, and diversity of the alpine plant communities of the region; 2) to obtain information on the soils associated with the major plant communities; 3) to acquire mesoclimatic data from several localities in the region; 4) to determine the interrelationships between soils, climate, and plant communities and use this to construct a comprehensive classification or ordination system for the alpine vegetation of the region; 5) to examine in detail several communities along an environmental gradient in a localized area (Grouse Ridge, Mt. Baker) and compare them with regard to their composition, structure, pattern, diversity, pedology, microclimate, phenology, physiology (water relations), and snowmelt pattern and 6) to relate the distribution of the North Cascadian alpine communities to other areas in Western North America.

STUDY AREA

Location

The Cascade Range, extending from southern Oregon to just north of the Washington-British Columbia border, can be subdivided into a number of ecological provinces on the basis of geology, soils, topography, climate, and vegetation. The northernmost of these provinces, the western and eastern North Cascades provinces (Douglas, 1972), were selected as the site of this study (Fig. 1). The area extends for about 130 km in a north-south direction, encompassing about 18,000 km².

The alpine zone, in this study, is defined as that area above the occurrence of trees in an upright form, and includes krummholz. The lower limit of the zone ranges from 1750 m on the west side of the range to 2100 m on the east side. The highest alpine vegetation found on the western side of the range was at 2176 m. This is probably the highest continuous vegetation occurring on the western slopes of the North Cascades since above this, and often at lower elevations, sheer rocky slopes, snowfields, and glaciers restrict the establishment of continuous vegetation. The upper limit of continuous alpine vegetation increases eastward, with the highest communities at about 2600 m on the eastern side of the North Cascades.

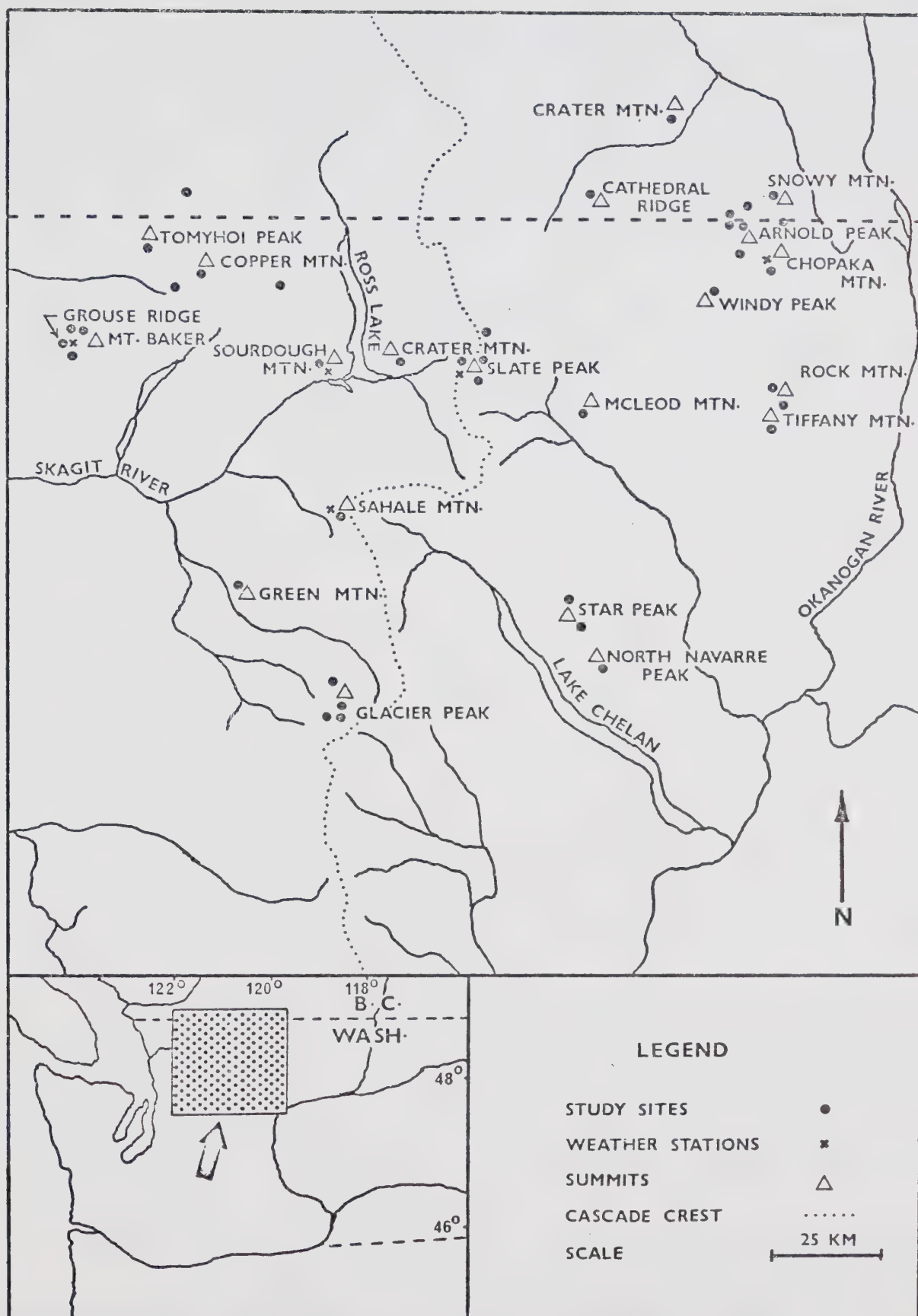


FIGURE 1. Map of the study sites in the North Cascades Range of Washington and British Columbia.

Geology and Geomorphology

The complex geologic history of the North Cascades has been studied in some detail by Misch (1952, 1966). The oldest rocks are crystalline basement rocks (mainly gneisses) which indicate an involved history of numerous igneous and metamorphic events. They predate the oldest known strata which consist of sedimentary and volcanic rocks, including Middle Devonian fossiliferous limestones. During the late Paleozoic era, depositions of clastic sediments took place on the floor of a vast shallow sea. These thick deposits were associated with a geosyncline that extended from Alaska to California. The clastic sediments include graywacke, shale, and sandstone. At this time volcanic eruptions also contributed basaltic and andesitic rocks to the deposition. These ancient geosynclinal rocks were then metamorphosed during a period of compression and folding, occurring simultaneously with the withdrawal of the sea during the Jurassic. Resulting metamorphic rocks include slate, phyllite, schist, and greenschist.

A new, smaller geosynclinal trough developed during early Cretaceous time, within which sedimentary rocks, including shale, siltstone, and sandstone were deposited. During Middle to early-Late Cretaceous time, major orogeny occurred in the North Cascades.

In the Tertiary further deposition, erosion, volcanism, and orogeny took place. During this time the granites, diorites, quartz diorites, and granodiorites in the central

and eastern parts of the range were formed. Final uplifting of the North Cascades took place in the Pliocene and subsequent weathering, mass wasting, and erosion contributed to the deeply dissected landscape of today. Schist, gneiss, and granite outcrops predominate throughout most of the range.

During late Pliocene and early Pleistocene time, the volcanic cones of Mt. Baker and Glacier Peak (elevations 3712 and 3181 m, respectively) were superimposed on the existing range (Coombs, 1939; Ford, 1959). Elsewhere in the Cascade Range the cones of Mt. Rainier, Mt. St. Helens, Mt. Adams, Mt. Hood, and Mt. Mazama were also being formed. The present cone of Mt. Baker was preceded by a higher volcano of which only the ruins (Black Buttes) remain (Coombs, 1939). These peaks consist mainly of andesite.

Although the period of major volcanic activity appears to have been at the beginning of the Pleistocene epoch, there were later eruptions and flows. In the North Cascades, ash layers originating from Glacier Peak, Mt. Mazama, and Mt. St. Helens have been recognized. The oldest of these ashfalls is that from Glacier Peak 12,000 years ago (Powers and Wilcox, 1964; Fryxell, 1965). This ash is distributed into southern British Columbia and east to Alberta and Montana (Wilcox, 1965; Westgate, personal communication). One of the most widespread ash layers, found from southern Oregon north to British Columbia and Alberta, and east to Montana, is that from Mt. Mazama (Wilcox, 1965; Nasmith *et*

al., 1967; Westgate and Dreimanis, 1967; Westgate *et al.*, 1969). The date of this eruption has been placed at about 6,600 years B.P. (Rubin and Alexander, 1960; Powers and Wilcox, 1964; Fryxell, 1965). Mt. St. Helens has erupted several times in the past 3,000 years producing ashfalls that have been dated at 3,000 and 500 years B.P. (Crandell *et al.*, 1962) and at 160 years B.P. (Mullineaux, 1964). This ash has an easterly and northerly distribution similar to that of the Mazama ash (Nasmith *et al.*, 1967; Westgate and Dreimanis, 1967; Westgate *et al.*, 1969). Mt. Rainier ash, dated at 2,300 and 2,000 years B.P. (Crandell *et al.*, 1962), may extend into the North Cascades although it has yet to be reported.

Although the major features of the North Cascades were produced prior to the Pleistocene epoch, massive continental ice sheets that flowed south into Washington, together with the marked expansion of the alpine glaciers in the local mountains, greatly modified the landscape. Evidence of this past glaciation can be seen throughout the range in the form of cirques, jagged ridges, steep-walled valleys, and the rounded tops of the lower mountains. Numerous, relatively small remnants of the once extensive alpine glaciers still remain in the region, which presently contains more active glaciers than any other North American region south of Alaska and Yukon.

The continental ice sheet and the alpine glaciers advanced and receded twice in the North Cascades during the

Salmon Springs Glaciation of the Late Pleistocene (early to middle Wisconsin) (Crandell, 1965). The broad, U-shaped valleys of the region were filled with ice during these advances.

The Fraser Glaciation, beginning with the Evans Creek Stade about 25,000 years B.P., lasted for approximately 15,000 years (Crandell, 1965) and resulted in the readvance of the alpine glaciers into the valleys. About 15,000 to 13,000 years B.P., after the alpine glaciers began to retreat, continental ice once again flowed into the North Cascades and reached its maximum development in western Washington and British Columbia. Toward the end of the Fraser Glaciation (Sumas Stade) and after a major recession of the continental ice, a colder climate prevailed once again with subsequent readvancement of the ice sheets and renewal of the alpine glaciers (Crandell, 1965). A mild Hypsithermal Interval followed the Fraser Glaciation during which time (*ca.* 10,000 to 5,000 years B.P.) the alpine glaciers decreased in size and mudflows and fluvial aggradations ensued throughout the range (Crandell, 1965). This warm period was followed by the last glaciation (Neoglaciation) which had its maximum development in the Cascade Range at varying times for different glaciers (Porter and Denton, 1967). Since the middle of the 19th century, glaciers in the region have generally been retreating, but around 1950 the Coleman Glacier on Mt. Baker, along with other glaciers in the range, began to advance (Bengsten,

1956).

Climate

The climate of the North Cascades varies considerably from maritime on the western slopes to more continental on the eastern slopes. This climatic difference, due to the prevailing westerlies from the Pacific Ocean crossing the large mountain massif, is most noticeable when examining the annual and summer (June - August) precipitation records from several weather stations. On the western side, the Diablo Dam station (elevation 272 m) has annual and summer averages of 189 and 14 cm, respectively, while annual and summer averages for the east side Winthrop (elevation 535 m) are 37 and 6 cm, respectively (U.S. Weather Bureau, no dates). Temperature records show corresponding differences (Fig. 2). Since very few weather stations exist in the region it is very likely, especially at higher elevations, that precipitation is greater and temperatures lower than illustrated here. This is evident at the Mt. Baker station (elevation 1265 m) in the western North Cascades which has annual and summer precipitation averages of 280 and 28 cm, respectively, and lower temperatures.

METHODS

Vegetation

A general reconnaissance of the alpine zone of the North Cascades was made in early summer 1970, as well as during a previous study (Douglas, 1972). From this survey tentative

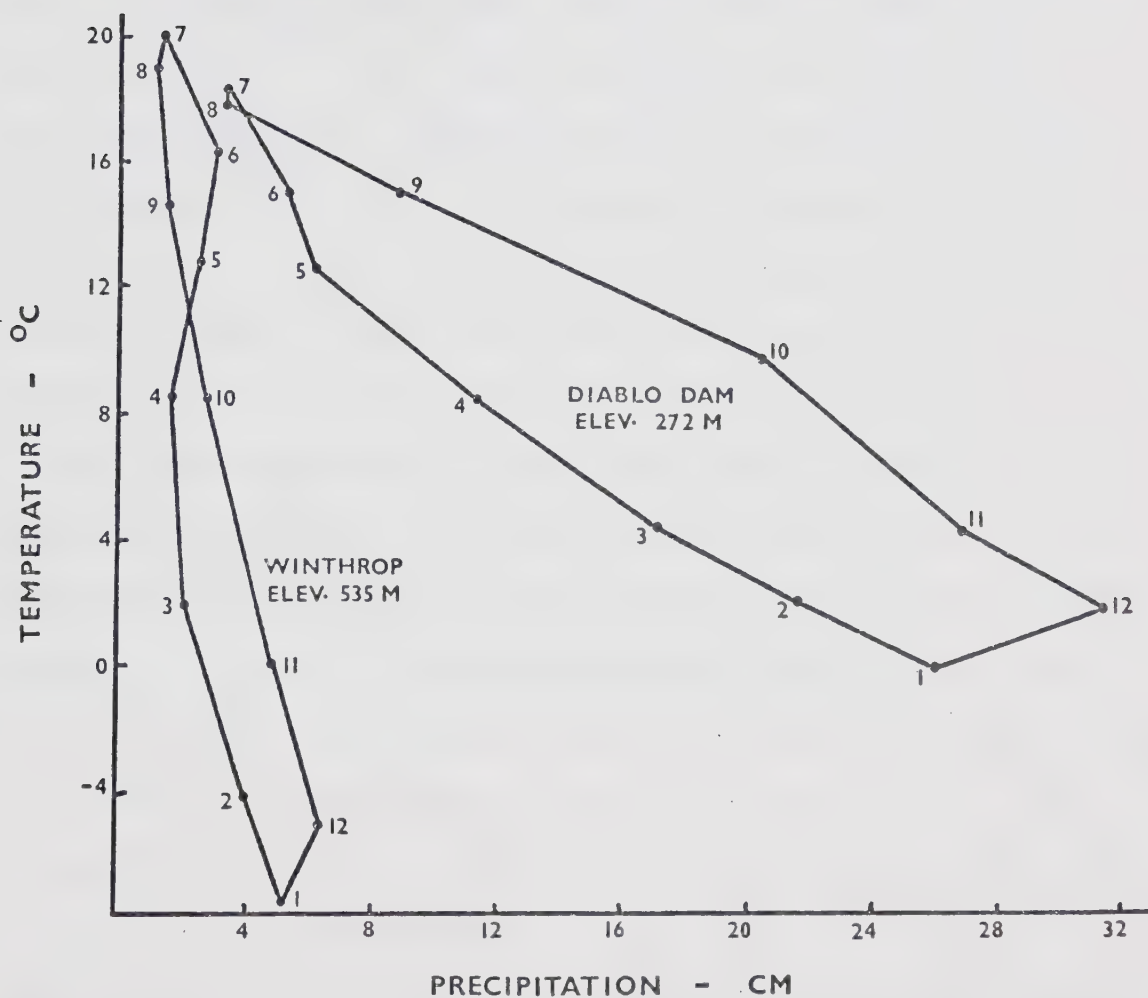


FIGURE 2. Temperature-precipitation climograph of mean monthly values at Diablo (western North Cascades) and Winthrop (eastern North Cascades) weather stations (data from U.S. Weather Bureau, no dates). Months are indicated by numbers beginning with January. Distance between the two stations is 45 km.

plant community types were delimited. Homogeneous stands representing the types were then selected for sampling. The term "stand", in this study, refers to a particular example of vegetation which was sampled, and "community" or "community type" to a grouping of similar stands. A total of 208 stands, varying in size from 150 to 1500 m², were sampled on 39 mountains in the study area (see Fig. 1). The community types are represented by 4 to 10 sampled stands. Rock outcrops and streamsides were not sampled.

For the regional survey, in examining all but the krummholz stands, twenty 20 X 50 cm quadrats were set out (perpendicular to the slope contours) by a restricted random technique (Bliss, 1963). Sampling replications were repeated three times for each of three stands differing in composition and structure. The replications indicated that, for all of the most prominent species, sampling was within $\pm 14\%$ of the mean prominence value for continuous vegetation and $\pm 26\%$ for discontinuous (fellfield) vegetation. The average coefficient of similarity was also computed for the replicates using the formula $C = 2w / (a + b) \times 100$ (Kulczynski, 1937), where w is the sum of the lowest prominence values of species common to both stands, and a and b are the total prominence values of all species in stands a and b . Stands of continuous vegetation had average similarity coefficients of 0.78 and 0.81 while the average fellfield similarity coefficient was 0.47. Sampling adequacy also met the "minimal area" criteria (Cain, 1938), with

sampling terminated, in almost all cases, well after the plateau in the species-area curve was reached. Minimum stand size was approximately 150 m².

Since krummholz stands were extremely variable, and because they were of secondary importance in this study, a more simplified procedure was necessitated to obtain general information on their structure and composition. These stands were examined by a "releve" method. Each stand was divided into four equal quarters and the crown cover for all species was estimated by visual observation in each quarter. Forty-two stands, varying in size from 25 to 100 m², were treated in this manner.

A third sampling procedure was used for analysis of species distribution along a 65 x 7 m belt transect on Grouse Ridge, Mt. Baker. At 2 m intervals down the slope, five 20 x 50 cm quadrats (from a possible 10), were randomly selected and set out at 5 dm intervals along and perpendicular to the slope contours.

Crown cover, using the methods and cover classes of Daubenmire (1959, 1968), was estimated by strata for all plant species (except epiphytic and epipetric cryptogams) in each quadrat. All additional rare species, which occurred outside the quadrats but within the stand, were also tallied. Frequency and average cover for each species were calculated and then converted to prominence values (PV) by multiplying the average percentage cover by the square root of the species frequency in each stand. This index has

been used in previous vegetation studies by Douglas and Ballard (1971), van der Valk and Bliss (1971), and Douglas (1972) and is a modification of the procedure used by Beals (1960). Similarity coefficients ($C = 2w / (a + b) \times 100$) between stands were then computed. Species were not adjusted in relation to their maximum values of frequency and cover as in Bray and Curtis (1957). Dissimilarity values ($1 - C$) were then computed and used for the construction of two-dimensional ordinations (Bray and Curtis, 1957; Beals, 1960). Several agglomerative hierarchical clustering techniques (Pritchard and Anderson, 1971) were also used for syntheses of stands.

The ordinations allowed the grouping of stands into community types that correlated with several environmental gradients. Although many of the community types, because of sharp environmental changes, occur as discrete vegetation units a number of them merge gradually with adjacent community types. This is reflected, in part, by the degree of separation between and within these types on the ordination. Community types are named after the one or two major dominants.

Cover data were used to compute the Shannon-Wiener general diversity index for each stand, $\bar{H} = \sum_{i=1}^S P_i \log_e P_i$ (Shannon and Weaver, 1949), where \bar{H} is the general diversity (richness and dominance concentration) and P_i is the cover value for each species divided by the total of cover values. The equitability or evenness index $E = \bar{H} / \bar{H} \max$ (Pielou,

1967) was also computed, where $\bar{H} \text{ max} = \log_e S$ and S is the number of species in the stand.

Nomenclature, authorities, and taxonomy follows Hitchcock and Cronquist (1973) for the vascular plants, Lawton (1971) for mosses, Schofield (1968) for hepatics, and Hale and Culberson (1970) for lichens, with the following exceptions. The treatment of *Claytonia lanceolata* Pursh follows Douglas and Taylor (1972), *Draba borealis* DC. and *D. ruaxes* Pays. & St. John follow Mulligan (1970, 1971), *Salix reticulata* L. ssp. *nivalis* (Hook.) Anderss. follows Love *et al.* (1971), and *Vaccinium uliginosum* L. ssp. *occidentale* (Gray) Hara var. *occidentale* follows Young (1970). The lichens *Cladonia gracilis* (L.) Willd. and *Peltigera canina* (L.) Willd. were not treated at the varietal level since the variants were often indistinguishable. *Thamnolia vermicularis* (Sw.) Ach. ex Schaer, has been included with *T. subuliformis* (Ehrh.) W. Culb. since they were indistinguishable in the field. Chemical tests revealed that 25 percent of all material collected was *T. vermicularis*. In the text only the binomial is used for any plant having just one variant in the North Cascades. A full set of voucher specimens has been placed in the University of Alberta herbarium (ALTA). Partial sets are in the Department of Agriculture (Ottawa) (DAO), New York Botanical Garden (NY), U.S. Forest Service (Fort Collins, Colo.), University of Washington (WTU), and Western Washington State College herbaria.

Soils

Soil pits were established in 16 different communities across the North Cascades and composite samples collected from each described horizon. Seven additional pits were also established along the environmental gradient at that study site in the western North Cascades. Samples were also collected from two additional soil pits opened by Bockheim (1972). Laboratory analysis of the fine (less than 2 mm) fraction included: texture by the hydrometer method (Bouyoucos, 1951); pH using a saturated paste (Doughty, 1941); and organic matter by the Walkley-Black wet oxidation method (Walkley and Black, 1934). Exchangeable cations were extracted with neutral N ammonium acetate and determined by atomic absorption spectrophotometry. Levels of N, P and K were determined at the Alberta Soil and Feed Testing Laboratory. Determination of N was done by the phenoldi-sulfonic method, P by the combined nitric acid, vanadate, molybdate colorimetric method, and K was extracted with N ammonium acetate at pH 7.0 and determined by flame photometry. Soil color was described for moist soil using the Munsell Color Charts in natural light.

Climate

Summer mesoclimate (*i.e.*, temperature, atmospheric moisture, solar radiation, precipitation, and wind) in the North Cascades was monitored at five different locations (see Fig. 1) during 1970, 1971, and 1972. Temperature and atmospheric moisture were monitored with Belfort and

Lambrecht hygrothermographs placed in white-painted, louvered shelters with sensors between 5 and 25 cm above the ground. Solar radiation was measured with Belfort actinographs set with sensors 10 cm above and parallel to the soil surface. Precipitation was measured with Tru-check rain gauges set 60 cm above and parallel to the soil surface. Wind was monitored with Belfort 3-cup totalizing anemometers with cups placed 60 cm above the ground.

Microclimate was monitored during the study period along the environmental gradient on Grouse Ridge. Four stations were established at 15 to 25 m intervals for a distance of 61 m down the slope. Soil and air temperatures were obtained by use of laboratory-calibrated RCA 1N2326 diodes, set in #3M Scotchcast No. 10 Electrical Resin. The soil temperature diodes were then placed in 13 mm (O.D.) aluminum pipe probes, sealed off, and buried horizontally at depths of 2, 10, 20, and 30 cm. The air temperature diodes were placed in double-shielded, open aluminum tubes, painted white outside and silver inside. These diodes were located at heights of either 5 and 15 cm or 10 and 20 cm; the latter heights being used for the taller vegetation at the base of the slope. Temperatures were measured with a bridge-meter powered by a mercury cell. Field measurements were precise within $\pm 0.5^{\circ}\text{C}$. Coleman soil moisture blocks (Coleman and Hendrix, 1949) were positioned in the same pits with the diodes at depths of 10 and 20 cm or 10 and 30 cm. Soil moisture was also determined periodically with

gravimetric samples taken at the same depths and within 2 m of the Coleman blocks. Soil samples from these same depths were collected and analyzed for percent moisture retention properties at 0.33 bars and 15 bars on ceramic plate extractors.

Phenology

Phenological stations were established at 10 m intervals along the 70 m belt transect on Grouse Ridge. Phenological notes were taken on 32 species at weekly intervals during 1971 and bi- to tri-weekly intervals during 1972. Observations, within a 2 x 2 m plot at each station, included the following phases: vegetative, flowering, fruiting, seed dispersal, and dormancy.

Physiology

Leaf water potential (ψ) was determined in the field during 1971 for 10 species on Grouse Ridge. A portable pressure chamber (Scholander *et al.*, 1964; Scholander *et al.*, 1965; Boyer, 1967) was used for these measurements. Leafy stems or leaves cut at the petiole were put directly into plastic bags from which all possible air was expressed. The bags were sealed, kept at ambient temperature out of direct sunlight, then measured within 0.5 hr of cutting. This procedure was found to have little, if any, effect on leaf ψ (Hickman, 1970). Measurements were made between 1300 and 1500 hr and at 2400 hr, times of near minimum and maximum leaf ψ , respectively.

RESULTS

Regional vegetation

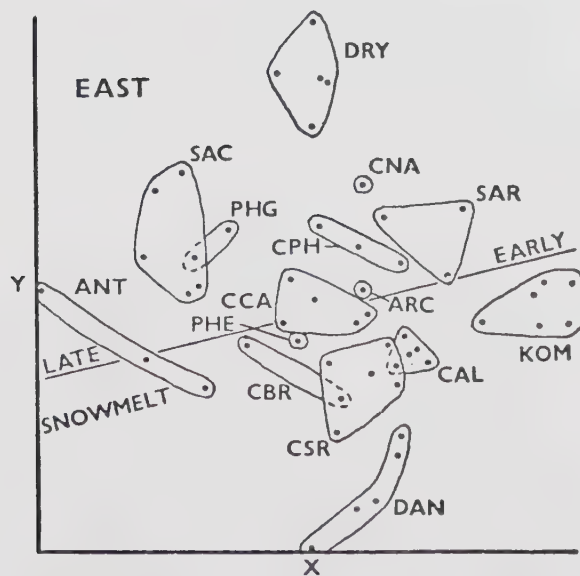
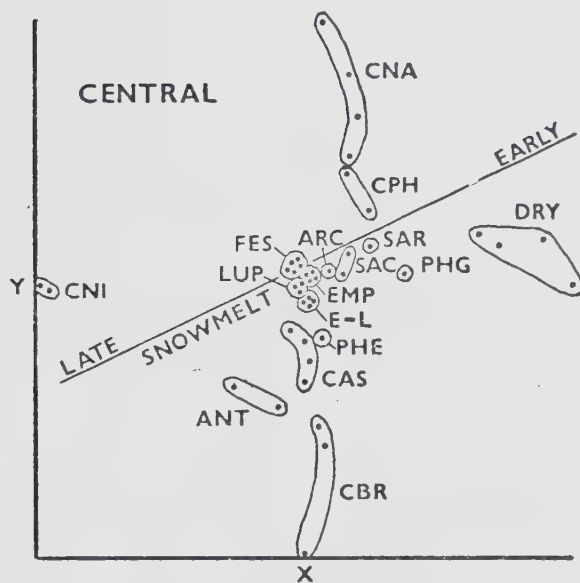
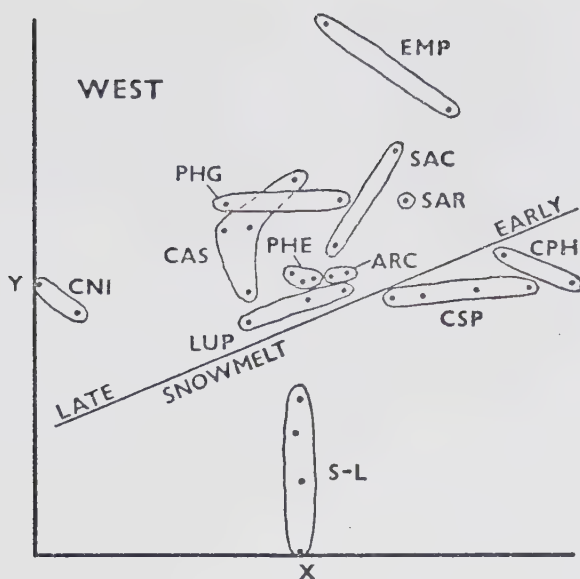
Two-dimensional ordinations (Bray and Curtis, 1957; Beals, 1960) were constructed, using prominence values, to provide an understanding of alpine community relationships and patterns (Fig. 3). Since high *beta* diversity, or a high degree of compositional change between communities along gradients (Whittaker, 1960), reduces ordination performance (Gauch and Whittaker, 1972) the North Cascadian communities have been treated within three separate regions (west, central, and east). Although the ordinations are based only upon floristic dissimilarities between samples stands, the stand groupings or community types do indicate some general environmental relationships. In this case, time of snow-melt is the most obvious environmental factor illustrated by the ordinations (Fig. 3). Twenty-three North Cascadian alpine community types and several other alpine vegetative units (krummholz and blockfields) are included in the following descriptions.

Snowbed community types

There are six community types in the North Cascades that are consistently associated with snowbed habitats. Several others, which are not restricted exclusively to snowbeds, but occur in them in at least part of their range, are discussed within the shrub community types.

a) *Saxifraga tolmiei*-*Luzula wahlenbergii* community.

Figure 3. Ordination of 128 stands in the alpine zone of the North Cascades. The stands are included in three ordinations, according to region (west, central, and east). Lines delimit community types whose names are derived from the dominant species. Abbreviations: S-L - *Saxifraga tolmiei*-*Luzula wahlenbergii*, E-L - *Eriogonum pyrolaeifolium*-*Luzula wahlenbergii*, CNI - *Carex nigricans*, ANT - *Antennaria lanata*, CBR - *Carex breweri*, CCA - *Carex capitata*, LUP - *Lupinus latifolius*, FES - *Festuca viridula*, CAS - *Cassiope mertensiana*, PHE - *Phyllodoce empetriiformis*, PHG - *Phyllodoce glanduliflora*, ARC - *Arctostaphylos uva-ursi*, EMP - *Empetrum nigrum*, SAR - *Salix reticulata*, SAC - *Salix cascadiensis*, DRY - *Dryas octopetala*, DAN - *Danthonia intermedia*, CAL - *Calamagrostis purpurascens*, CSP - *Carex spectabilis*, CPH - *Carex phaeocephala*, CSR - *Carex scirpoidea* var. *pseudoscirpoidea*, CNA - *Carex nardina*, KOB - *Kobresia myosuroides*.



This community occurs on gentle to moderately steep, mainly southerly slopes in the western North Cascades (Fig. 4). Snow remains in these habitats until late July or early August. Soils are poorly developed, poor to fairly well drained, and show indications of surficial movement.

The *Saxifraga-Luzula* community is characterized by a low average total plant cover (33%) and an average of only 8 species (18 in total) per stand. *Saxifraga tolmiei* and *Luzula wahlenbergii* are the only constant species with mean covers of 15% and 7% and frequencies of 78% and 35%, respectively. Other less prominent plants are *Carex pyrenaica*, *Juncus drummondii*, *Polytrichum sexangulare*, and *Marsipella brevissima*.

b) *Eriogonum pyrolaeifolium-Luzula wahlenbergii* community. In the central North Cascades (Fig. 4) this community type is most commonly found on slight to moderately steep, northerly slopes. The habitat is similar to the *Saxifraga-Luzula* type found farther west. Snowmelt is late (early to late July) and soil surfaces are unstable. These sites, in contrast to the *Saxifraga-Luzula* habitats, are well drained and are more xeric in late summer.

This community type, with an average total plant cover of 17% (Table 1), is the most sparsely vegetated of all the major alpine ones examined. An average of 15 species per stand (32 in total) occur in this community. *Eriogonum pyrolaeifolium* and *Luzula wahlenbergii*, with low mean covers (6% and 3%, respectively) and frequencies (68% and 29%,

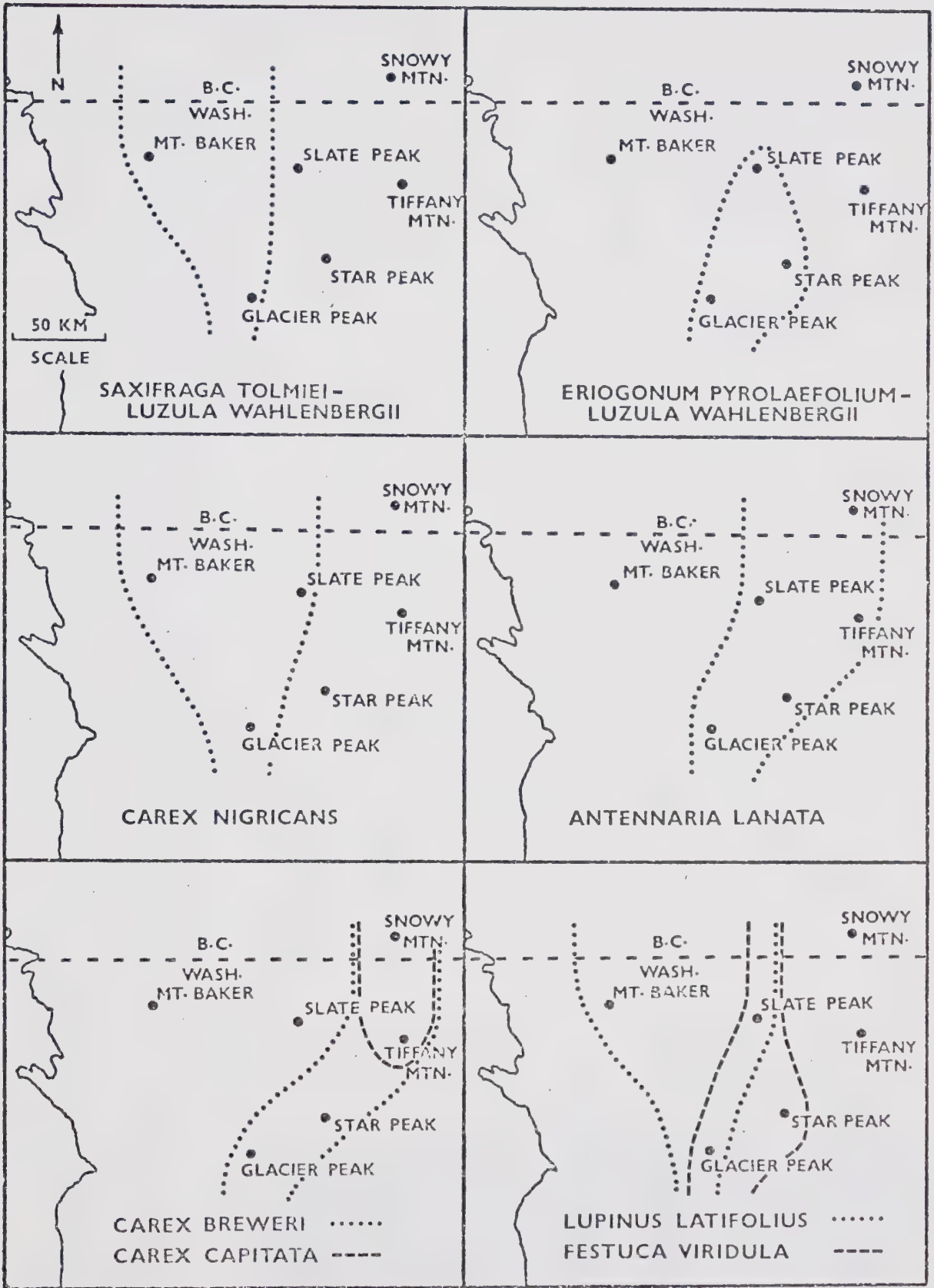


FIGURE 4. Distribution of snowbed and lush herb community types in the North Cascades Range.

Table 1. (continued)

Species	Community types																						
	S-L	E-L	CNI	ANT	CBR	CCA	LUP	FES	CAS	PHE	PHG	ARC	ETP	SAR	SAC	DRY	DAN	CAL	CSP	CPH	CSR	CNA	KOM
<u>Lycopodium sitchense</u>	3												3										
<u>Cassiope tetragona</u>	2														P								
<u>Arctostaphylos uva-ursi</u>	1												615	3	T								
<u>Pedicularis groenlandica</u>	T																						
<u>Lycopodium alpinum</u>											15												
<u>Picea engelmannii</u>											6					P							
<u>Juniperus communis</u>											1				P	1							P
<u>Saxifraga bronchialis</u>											T				T	P	2						
<u>Senecio cybalarioides</u>											T												
<u>Gentiana glauca</u>											T												
<u>Abies lasiocarpa</u>											T												
<u>Saxifraga tetradactyla</u> var. <u>macounii</u>											T												1
<u>Carex albigena</u>											13				T	3	5	1		T	4		
<u>Draba olivacea</u>											2				1	T		T		1			
<u>Eriogonum ovalifolium</u> var. <u>nivale</u>											1									1			
<u>Potentilla nivea</u>											1				1		T	4					P 1
<u>Draba pavsonii</u>											1				T					1			T 1
<u>Lupinus caritophorum</u>											T				T			L		2	2		T 1
<u>Phacelia sericea</u>											T									T			
<u>Campanula rotundifolia</u>											P		6	T						37	1		
<u>Cassiope stelleriana</u>													19										
<u>Carex bruchmannii</u>													2										
<u>Agrostis scabra</u>													1										1 1
<u>Potentilla villosa</u>														T									T
<u>Dodecatheon pauciflorum</u> var. <u>watsonii</u>														T									
<u>Saxifraga occidentalis</u> var. <u>occidentalis</u>																							T
<u>Penstemon davidsonii</u> var. <u>davidsonii</u>															1		T			3			P
<u>Poa gracillima</u>																							1
<u>Androsace septentrionalis</u>															T		T	T		T	2		3
<u>Arcyria rubella</u>																	T	1					1
<u>Draba ruaxes</u>															T								
<u>Vaccinium uliginosum</u> var. <u>occidentale</u>															P								
<u>Arctostaphylos nevadensis</u>																1							
<u>Potentilla uniflora</u>																1							
<u>Potentilla fruticosa</u>																1		P					6
<u>Orizopsis exigua</u>																							
<u>Polemonium elegans</u>																T							
<u>Draba lonchocarpa</u> var. <u>lonchocarpa</u>																T							1
<u>Silene douglasii</u>																							
<u>Draba borealis</u>																	14						
																	T						1

Table 1. (continued)

Species	Community types																						
	S-L	E-L	CNI	ANT	CBR	CCA	LUP	FES	CAS	PHE	PHG	ARC	ETP	SAR	SAC	DRY	DAN	CAL	CSP	CPH	CSR	CNA	KOM
<i>Poa gravana</i>																		T					
<i>Thalictrum</i> sp.																		T	9				
<i>Fragaria virginiana</i>																				5			
<i>Geum triflorum</i>																				3		P	
<i>Antennaria luzuloides</i>																				1		4	
<i>Antennaria microphylla</i>																				T			
<i>Arabis hoebelii</i> var. <i>pendulocarpa</i>																						2	
<i>Fraxinus corymbosa</i> var. <i>discoideus</i>																						T	
<i>Sedum umbellata</i> var. <i>caudicifera</i>																							P
<i>Douglasia nivalis</i>																							
BRYOPHYTES																							
<i>Polypodium sexangulare</i>	10			11														T					
<i>Ureopeltis brevissima</i>	10																						
<i>Cladonia hercynicum</i>	1			T 18					1	T								T	1				
<i>Pohlia nutans</i>	1									2													
<i>Dicranum montanum</i>	P																						
<i>Distichum capillaceum</i>																							
<i>Polypodium piliferum</i>																							
<i>Phacelium canescens</i> var. <i>ericoides</i>	2																						
<i>Polypodium juniperinum</i>	1			50	6	85																	
<i>Polypodium adelphus lyallii</i>				74	2	22																	
<i>Klaeria blyttii</i>				36		70																	
<i>Lezourea radicans</i>				24																			
<i>Dicranum spadicum</i>				14																			
<i>Bryum</i> cf. <i>angustifolium</i>				11	3	3																	
<i>Desmatodon latifolius</i> var. <i>latifolius</i>																							
<i>Tortula ruralis</i>																							
<i>Andropogon palustris</i>																							
<i>Bryum</i> sp.																							
<i>Hilcomium splendens</i>																							
<i>Dicranum muhlenbeckii</i>																							
<i>Drepanocladus uncinatus</i>																							
<i>Bryum</i> cf. <i>pallens</i>																							
<i>Ceratodon purpureus</i>																							
<i>Bryum</i> cf. <i>cyclophyllum</i>																							
<i>Hypnum revolutum</i>																							
<i>Tortula norvegica</i>																							
<i>Brachythecium starkeri</i>																							
<i>Lophozia hatcheri</i>																							
<i>Bryum caespitium</i>																							
<i>Dicranum fuscescens</i>																							

Table 1. (continued)

Species	Community types																							
	S-L	E-L	CNI	ANT	CBR	CCA	LUP	FES	CAS	PHE	PHG	ARC	EMP	SAR	SAC	DRY	DAN	CAL	CSP	CPH	CSR	CNA	KOM	
<u>Buellia epizaca</u>					T	2								1	1		T	2				22	1	
<u>Caloplaca tetraspora</u>					T									4		T	3	6		T	1	T	6	
<u>Cetraria arictorum</u>						40	T						13	19	1	T	12	32	54	38	14	1	30	
<u>Cladonia fraxinodens</u>					6																			
<u>Cetraria cucullata</u>					1											T	T	26		2	5		55	
<u>Cladonia bellidiflora</u>										6	11							2		T		T	1	
<u>Diploschistes seruposus</u>										17	T													
<u>Cladonia subsquamosa</u>											21													
<u>Cladonia coccinea</u>											6											T		
<u>Pinodina malacea</u>																								
<u>Buellia zahlbruckneri</u>											6													
<u>Cladonia squamosa</u>											T													
<u>Caloplaca lungermanniae</u>											T	2		T	T	1				T	T			
<u>Psoralea hyporum</u>														T	T	T								
<u>Peltigera malacea</u>																								
<u>Stereocaulon sp.</u>																1							1	
<u>Camptelaria cf. canadensis</u>																T	1	T						
<u>Physconia muscigena</u>																			5		6	1		
<u>Cladonia fibrillata</u>																			1					
<u>Cladonia cariosa</u>																								
<u>Cladonia phyllophora</u>																				T		T		
<u>Caloplaca stillicidiorum</u>																				T		T		
<u>Leclion sp.</u>																								
<u>Peltigera sp.</u>																					T			
<u>Lecanora epibryon</u>																						T		
TOTAL COVER (%)	29	14	126	82	82	137	137	192	120	89	76	73	114	81	63	44	40	194	146	149	99	113	57	148
Vascular species	4	2	18	26	23	35	2	3	4	11	11	11	2	3	8	10	2	12	6	22	13	19	6	23
Bryophytes																								
Lichens		1	8	29	26	17	3	1	17	8	30	3	14	20	19	9	13	28	39	31	24	20	40	
Bareground	21	58	2	4	11	4	9	26	12	12	16	13	19	12	25	19	5	6	16	9	7	26	3	
Rocks	56	27		1	5	1			6	7	6	6	1	21	9	41	6	15	10	6	15	8		
All plants	33	17	152	137	131	189	197	124	110	95	114	119	98	91	73	51	219	180	210	143	156	83	211	

Table 1. (continued)

Community types																								
S-L		E-L	CNI	ANT	CBR	CCA	LUP	FES	CAS	PHE	PHG	ARC	EMP	SAR	SAC	DRY	DAN	CAL	CSP	CPH	CSR	CNA	KOM	
TOTAL NUMBER OF SPECIES																								
10		21	15	37	46	36	48	39	35	35	51	44	42	51	46	48	42	44	35	61	43	44	42	
6		3	6	6	10	14	2	6	9	6	7	5	6	15	11	4	7	6	13	18	13	8	7	
2		8	7	14	18	20	6	2	12	15	24	10	13	16	22	25	16	14	13	22	23	18	17	
18		32	28	57	74	70	56	47	56	56	82	59	61	82	79	77	65	64	61	101	79	70	66	
AVERAGE NUMBER OF SPECIES																								
5		12	9	15	16	20	17	24	13	14	17	18	12	22	16	17	25	25	18	21	22	20	27	
2		2	2	3	4	6	0	2	3	3	3	2	2	4	3	2	3	4	5	4	4	2	6	
1		2	2	7	7	9	1	1	4	6	10	3	4	12	10	10	8	12	7	9	9	10	12	
8		15	14	25	27	35	18	27	20	22	30	23	18	38	28	28	36	41	30	34	35	32	44	

a. Abbreviations: S-L - *Saxifraga tolmiei*-*Luzula wahlenbergii*, E-L - *Eriogonum pyrolaeifolium*-*Luzula wahlenbergii*, CNI - *Carex nigricans*, ANT - *Antennaria lanata*, CBR - *Carex breweri*, CCA - *Carex capitata*, LUP - *Lupinus latifolius*, FES - *Festuca viridula*, CAS - *Cassiope mertensiana*, PHE - *Phyllocladus ericifolius*, PHG - *Phyllocladus glanduliflora*, ARC - *Arctostaphylos uva-ursi*, EMP - *Empetrum nigrum*, SAR - *Salix reticulata*, SAC - *Salix cascadiensis*, DRY - *Draba octopetala*, DAN - *Danthonia intermedia*, CAL - *Calamagrostis purpurascens*, CSP - *Carex spectabilis*, CPH - *Carex phaeocephala*, CSR - *Carex scirpoidea* var. *pseudoscirpoidea*, CNA - *Carex nardina*, KOM - *Kobresia myosuroides*; I (trace) indicates a mean prominence value of less than 0.5, P (present) indicates that a species was present but not tallied in the community type.

b. Number of stands sampled are enclosed in parentheses.

respectively) are the only constant species.

c) *Carex nigricans* community. Concave to level, poorly drained sites are typical of this community throughout its western to central range in the North Cascades (Fig. 4). This snowbed type has the greatest snow accumulation and shortest snowfree period of all habitats in the region, with snow persisting until late July or early August, or in years of high snowfall, early September. Soils are poorly drained and remain moist for most of the summer.

Carex nigricans forms a low, dominant mat with a high average cover (75%) and frequency (95%). Twenty-eight species (average of 14 per stand) are found in this type. Other prominent species are *Luetkea pectinata* and *Deschampsia atropurpurea* (Table 1). *Polytrichadelphus lyallii*, *Kiaeria blyttii*, *Lescurea radicata*, and the lichen *Lepraria neglecta* are important cryptogams.

d) *Antennaria lanata* community. Communities of this type are found from the central to eastern North Cascades (Fig. 4) in snowbed habitats (Fig. 5) similar to those of the *Carex nigricans* type. In the central North Cascades, where the ranges overlap, the two communities may be found adjacent to each other. The *Antennaria* type, however, becomes snowfree two to four weeks earlier (late June to late July) and since the soils have better drainage the sites become drier during late summer.

The total mean plant cover (137%) of the *Antennaria* community is similar to that of the *Carex nigricans*

Figure 5. An *Antennaria lanata* community in a slight depression at 2180 m on Crater Mountain, Washington. The *Cassiope mertensiana* community occurs on the adjacent slopes.



community but a greater contribution is made by mosses and lichens in the former. The *Antennaria* community is also floristically richer with an average of 25 species per stand and a total of 57. *Antennaria lanata*, the dominant species in the type, has a frequency of 100% and a mean cover of 35%. *Carex nigricans* and *Leutkea pectinata* are important components in the central North Cascades with *Salix cascadiensis* and *Carex scirpoidea* var. *pseudoscirpoidea* becoming prominent farther east. *Polytrichum piliferum* and *Lepraria neglecta* are common cryptogams throughout the range while *Cetraria islandica* becomes important in the eastern North Cascades.

e) *Carex breweri* community. This snowbed type occurs mainly in concave sites in the eastern North Cascades although several stands were encountered on slight slopes just south of Glacier Peak (Fig. 4). These sites are snow-free by the latter part of July, are well drained, and become dry during late summer. This is reflected, in part, by the large number of xerophytic alpine species in the type (e.g., *Carex scirpoidea* var. *pseudoscirpoidea*, *C. nardina*, etc.).

A total of 74 species and an average of 27 per stand are found in this community. *Carex breweri*, the major species, has an average cover of 32% and frequency of 92%. *Erigeron aureus*, *Lupinus lepidus* var. *lobbii*, and *Danthonia intermedia* occur with moderate frequency and relatively low cover. Prominent cryptogams are *Polytrichum piliferum*,

Kiaeria blyttii, *Lepraria neglecta*, and *Cetraria islandica* (Table 1).

f) *Carex capitata* community. This is a common type at higher elevations (2300 m to 2450 m) in the eastern North Cascades (Fig. 5). This community occurs in level to slightly concave sites that are often dominated by hummocky topography (Fig. 6). Of all the snowbed types in the region the *Carex capitata* community generally has the lowest snow accumulation and is the first to become snowfree (June) although soils, due to drainage from upslope, remain moist well into the summer.

Communities of this type have an average total plant cover of 189% including an average bryophyte cover of 35%, the highest of any snowbed community in the region (Table 1). Seventy species (average of 35 per stand) occur in this community. *Carex capitata* is the dominant species with a mean cover of 57% and a frequency of 100%. Important vascular plants are *Potentilla diversifolia* var. *diversifolia*, *Solidago multiradiata*, *Salix cascadiensis*, *Festuca ovina* var. *brevifolia* and *Carex scirpoidea* var. *pseudoscirpoidea* (Table 1). Prominent mosses and lichens are *Dicranum muehlenbeckii*, *Polytrichum juniperum*, *Cetraria ericetorum*, and *Cladonia pyxidata*.

Lush herb community types

Two of the North Cascadian alpine communities are included within the lush herb types. These communities are characterized by a dense cover of mesophytic herbs and

Figure 6. A *Carex capitata* community at 2380 m on Arnold Peak, Washington. The *Carex scirpoidea* var. *pseudoscirpoidea* community covers the extensive slopes in the background.



usually lack a cryptogamic stratum.

a) *Lupinus latifolius* community. The *Lupinus* type is found at lower elevations (1750 m to 2150 m) in the western to central North Cascades (Fig. 4). It occurs most frequently on moderate to steep southerly, well drained slopes (Fig. 7), and is often found adjacent to, or just below stands of krummholz. Snowmelt is relatively early (late May to early June).

The *Lupinus* community is characterized by a dense cover (192%) of mesophytic herbs and sedges. An average of 18 species (56 in total) occur in this community. *Lupinus latifolius* var. *subalpinus*, the most prominent species in the type, has a frequency of 100% and a mean cover of 62%. *Carex spectabilis*, *Polygonum bistortoides*, *Vaccinium deliciosum*, *Festuca viridula*, *Erigeron peregrinus* var. *scaposus*, and *Valeriana sitchensis* are major associates (Table 1).

b) *Festuca viridula* community. This community type is apparently restricted to lower elevations (1850 m to 2150 m) on southerly, well drained slopes in the central North Cascades. These slopes become free of snow about the same time as in the *Lupinus* habitats but soils become drier during late summer.

This community is closely related to the *Lupinus* type with a large number of species common to both (Table 1). Total vascular plant cover (120%) is much lower, however, and *Lupinus latifolius* is replaced by *Festuca viridula* as

Figure 7. A *Lupinus latifolius* community at 1980 m on
Glacier Peak, Washington. The *Empetrum nigrum*
occurs on the adjacent upper slopes.



the dominant. A total of 47 species and an average of 27 per stand are found in this type. *Festuca viridula* has a relatively high average cover and frequency of 48% and 96%, respectively. Other important plants are *Antennaria lanata*, *Arenaria capillaris*, *Agoseris glauca* var. *dasycephala*, *Lupinus latifolius* var. *subalpinus*, *Potentilla flabellifolia*, *Juncus parryi*, and *Arnica rydbergii* (Table 1).

Dwarf Shrub community types

In the North Cascades eight dwarf shrub community types occur in a variety of habitats. This group contains five of the six community types which range across the entire North Cascadian region.

a) *Cassiope mertensiana* community. This is one of the most common communities in the western North Cascades. Its range extends east to the Slate Peak and Glacier Peak areas in the central part of the range (Fig. 8). Mesic, well drained, moderately steep to steep, southerly slopes are typical sites of this type. This community is closely related to the *Phyllodoce empetriformis* and *P. glanduliflora* types (Fig. 3). In the subalpine zone of the western North Cascades, *Cassiope mertensiana* and *Phyllodoce empetriformis* commonly occur together as co-dominants (Douglas, 1972).

The *Cassiope* community has an average total plant cover of 110% and an average of 20 species (56 in total) per stand. The dominant species is *Cassiope mertensiana*, which occurs with 94% frequency and 42% average cover. *Luetkea*

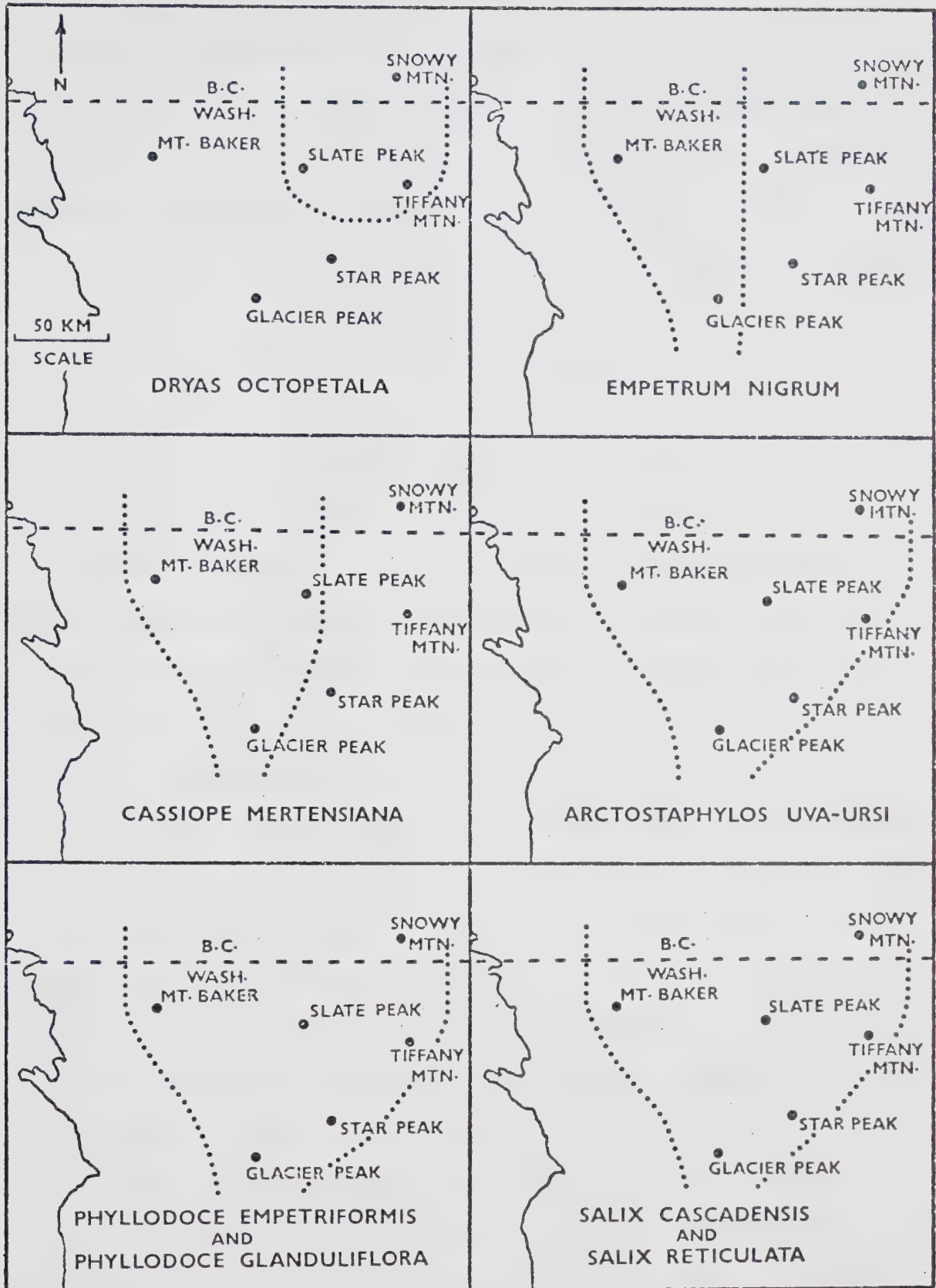


Figure 8. Distribution of dwarf shrub community types in the North Cascades Range.

pectinata, *Phyllodoce glanduliflora*, *Antennaria lanata*, and *Vaccinium deliciosum* are important associates; the latter being restricted mainly to the western North Cascades. In the central part of the region *Phyllodoce empetriformis* becomes prominent. *Lepraria neglecta* is the major cryptogam with *Cetraria islandica* and *Polytrichum piliferum* occurring frequently, but with low cover.

b) *Phyllodoce empetriformis* community. This type is found on sites that appear quite similar to those of the *Cassiope* type, at least in the western and central Cascades where both are extremely common. At the eastern extent of its range (Fig. 8) it is restricted to slight snowbed depressions in the lower alpine zone. Snowmelt in this drier region of the Cascades occurs at approximately the same time (early June to early July) as in the more exposed central and western habitats.

The *Phyllodoce* community has an average of 22 species (56 in total) per stand and an average total plant cover of 95%. *Phyllodoce empetriformis* is the major species with a mean cover of 34% and a frequency of 82%. Other prominent species are *Antennaria lanata* (occurring across the entire range), *Vaccinium deliciosum* and *Cassiope mertensiana* (both restricted to the western and central Cascades) and *Vaccinium scoparium* (found from the central to eastern Cascades). *Polytrichum piliferum* and *Lepraria neglecta* are conspicuous cryptogams in most *Phyllodoce empetriformis* stands while *Dicranum fuscescens* is important in the western

North Cascades.

c) *Phyllodoce glanduliflora* community. The more exposed, upper slopes are typical sites of this community type in the western North Cascades. Farther east the type occurs in more protected habitats although time of snowmelt is similar (early to late June). This type occurs on all aspects and soils range from well drained, on straight slopes, to more poorly drained on hummocky terrain.

Floristically, the *Phyllodoce glanduliflora* community is the richest of the heath types with a total of 82 species and an average of 30 per stand. Average total plant cover is 114%. The community is dominated by *Phyllodoce glanduliflora* which has a frequency of 89% and an average cover of 36%. *Vaccinium deliciosum* and *Leutkea pectinata* are important associates in the western North Cascades while *Antennaria lanata* and *Salix cascadiensis* become prominent components in the eastern stands. Moss and lichen cover (41%) is the highest of all heath types. Important cryptogams throughout the range are *Cetraria islandica*, *Lepraria neglecta*, and *Polytrichum piliferum*. In the eastern North Cascades the moss, *Dicranum scoparium* becomes conspicuous.

d) *Arctostaphylos uva-ursi* community. The *Arctostaphylos* community is found mainly on southerly sites where soils are generally poorly developed, but well drained. It occurs infrequently throughout the North Cascades. Snowmelt is moderately early, occurring from late May to mid-June.

Arctostaphylos uva-ursi is the sole dominant (mean

cover 63% and frequency 92%), except in the western North Cascades where *Carex spectabilis* is an important associate. The high cover and dominance of *Arctostaphylos* limits other species, and especially cryptogams, to a low prominence in the type. Fifty-nine species (average of 23 per stand) occur in this type.

e) *Empetrum nigrum* community. This community type occurs on moderately steep, well drained, south to west slopes at lower elevations (1750 m to 2100 m) in the western to central North Cascades (Fig. 8). Time of snowmelt (late May to mid-June) is similar to that in the heath types.

Sixty-one species (average of 18 per stand) occur in the *Empetrum* community. The major species is *Empetrum nigrum* with a high average cover of 52% and frequency of 97%. *Phyllodoce glanduliflora*, although a common associate, occurs with low cover and frequency. In the Glacier Peak area *Lupinus lepidus* var. *lobbii* becomes prominent in the community. *Cetraria islandica* is the only prominent and constant cryptogam.

f) *Salix reticulata* community. Communities of this type occur throughout the region (Fig. 8) on level to moderately steep, exposed, southerly slopes. The soils of these types are extremely rocky and often show indications of frost action (i.e., unsorted nets, frost boils). Snowmelt is relatively early, generally occurring between mid-May and early June.

The *Salix reticulata* community has an average of 38

species per stand and a total of 82. The most important species in this type is *Salix reticulata* ssp. *nivalis* with a mean cover of 31% and a frequency of 92%. *Festuca ovina* var. *brevifolia* and *Selaginella densa* are constant associates in all stands (Table 1) while *Oxytropis campestris* var. *gracilis* becomes important in the eastern part of the region. The lichens, *Thamnolia subuliformis*, *Cornicularia aculeata*, *Cetraria islandica*, *Lepraria neglecta* are frequent throughout the range. *Polytrichum juniperinum* and *Desmatodon latifolius* are important mosses in the eastern North Cascades.

g) *Salix cascadiensis* community. In the western North Cascades this community is found on sites similar to those of the *Salix reticulata* community. In the eastern part of its range, however, the *Salix cascadiensis* type occurs on gentle slopes or level sites of all aspects and often occupies snowbed habitats. Although the latter habitats become snowfree later (early June) than those on exposed sites drainage is good and the habitats become quite dry.

Salix cascadiensis, the dominant species, occurs with relatively high average cover (35%) and frequency (83%). An average of 28 species per stand (79 in total) are found in this type. Species composition is more variable than in the *Salix reticulata* type. Throughout the range *Festuca ovina* var. *brevifolia* and *Carex phaeocephala* are characteristic components. *Erigeron aureus* and *Arenaria obtusiloba* are important in the central and eastern North Cascades. In

the Glacier Peak area *Lupinus lepidus* var. *lobbii* is a conspicuous associate. The prominent cryptogams in most stands are *Polytrichum piliferum*, *Cetraria islandica*, and *Lepraria neglecta*.

h) *Dryas octopetala* community. The *Dryas* type occurs on slight to moderate slopes of all aspects from the central to eastern North Cascades (Fig. 8). These sites usually have well drained, poorly developed soils (Fig. 9). Snow-melt is relatively early (early to late May).

This community has one of the lowest total plant covers (50%) of all types in the region (Table 1). Seventy-seven species (average of 28 per stand) occur in this type. *Dryas octopetala* is the major species with a mean cover of 23% and frequency of 80%. Typical associates, with low prominence, are *Lupinus lepidus* var. *lobbii*, *Arenaria obtusiloba* and *Festuca ovina* var. *brevifolia*. Many cryptogams occur frequently in this type but all are of low importance (Table 1).

Dry grass community types

Two communities, both restricted to the eastern North Cascades, are included in the dry grass types. These communities are characterized by high total plant cover and dominance by grass species.

a) *Danthonia intermedia* community. Communities of this type cover large expanses in the lower alpine and subalpine zones of the eastern North Cascades (Fig. 10). The moderate to steep slopes are well drained and receive moisture from

Figure 9. A *Dryas octopetala* community at 2410 m on Windy Peak, Washington. Plant cover is relatively low on these dry sites.



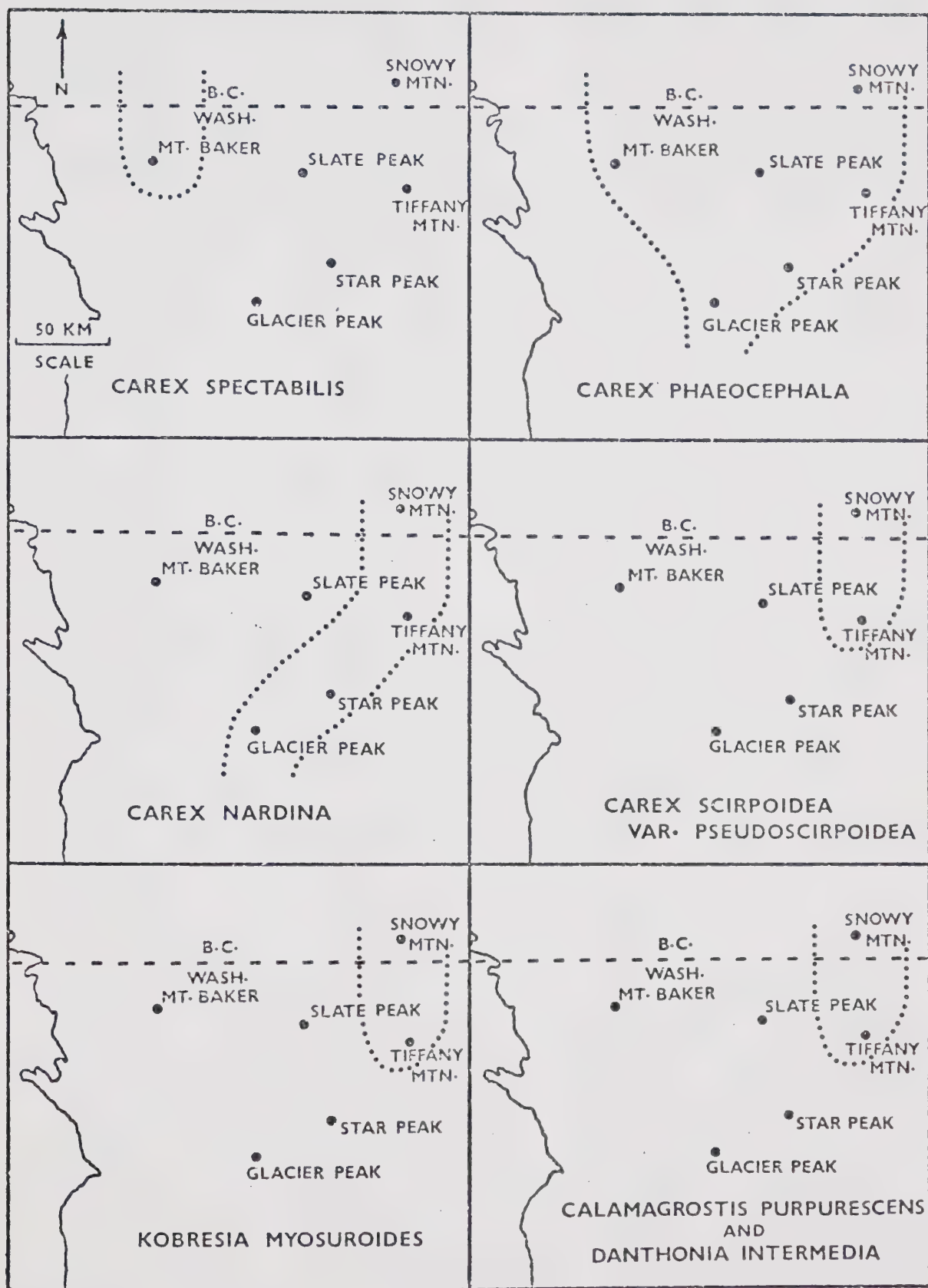


Figure 10. Distribution of dry sedge and dry grass community types in the North Cascades Range.

upslope for much of the summer. Snowmelt takes place from mid-May to early June.

The total average plant cover (219%) in this type is the highest in the alpine zone. *Danthonia intermedia* has a high frequency (99%) and average cover (56%), and it dominates all stands. Many associates, such as *Carex scirpoidea* var. *pseudoscirpoidea*, *Potentilla diversifolia* var. *diversifolia*, *Arenaria capillaris* and *A. obtusiloba* also have high prominence values (Table 1). An average of 36 species per stand (65 in total) are found in this type. Common cryptogams are *Polytrichum juniperinum*, *P. piliferum*, *Tortula ruralis*, *Cetraria islandica* and *Cladonia pyxidata*.

b) *Calamagrostis purpurascens* community. Small stands of this community type are frequent at higher elevations (over 2250 m) in the eastern North Cascades (Fig. 6). Slopes are moderate to steep, well drained, and often rocky. Snow accumulation is slight with snowmelt occurring relatively early (April to early May).

Calamagrostis purpurascens is the dominant species (mean cover 38% and frequency 97%) and is common only to this type. Sixty-four species (average of 41 per stand) occur in this type. *Carex scirpoidea* var. *pseudoscirpoidea*, *Arenaria obtusiloba*, *Oxytropis campestris* var. *gracilis*, and *Potentilla diversifolia* var. *diversifolia* are prominent species (Table 1). *Cornicularia aculeata*, *Cladonia pyxidata*, *Cetraria ericetorum*, and *C. islandica* are the most conspicuous of the large number of lichens present.

Polytrichum juniperinum is the only constant moss of importance.

Dry sedge community types

The dry sedge types are probably the most characteristic alpine communities in the region, especially in the eastern North Cascades. These types are found on the drier slopes of their particular ranges. Five dry sedge communities are recognized in this study.

a) *Carex spectabilis* community. This community type is restricted to drier, moderately steep to steep, upper slopes in the western North Cascades (Fig. 10). These southerly, well drained habitats are free of snow relatively early (mid-May to early June).

Total average plant cover (210%) is one of the highest of all the alpine types in the region. A total of 61 species and an average of 30 per stand are found in this type. *Carex spectabilis* is the sole dominant with a high average cover of 55% and frequency of 100%. Other prominent species are *Solidago multiradiata*, *Valeriana sitchensis* and *Carex breweri* (Table 1). Cryptogamic cover is high (61%) with *Cladonia gracilis*, *Cladina mitis*, *Cetraria ericetorum* and *Polytrichum piliferum* being major components.

b) *Carex phaeocephala* community. This type is common on moderately steep to steep, well drained, upper slopes in the western North Cascades. Farther east it becomes less frequent and often grades into the closely related *Carex scirpoidea* var. *pseudoscirpoidea* community. The *Carex*

phaeocephala community occurs mainly on southerly aspects although several stands in the eastern North Cascades were encountered on northwest or northeast aspects. In the western North Cascades this is the first major plant community to become free of snow while in the eastern part of the region, although snowmelt is about the same (May), several other types precede it.

Carex phaeocephala, with a moderately high mean cover (27%) and high frequency (97%), is the most prominent species in the community. Floristically, this is the richest (a total of 101 species and an average of 34 per stand) and most variable type in the region. In the western stands *Phlox diffusa* is a major associate. *Lupinus lepidus* var. *lobbii* is important only in the central North Cascades while *Arenaria obtusiloba* is common here as well as farther east. *Carex scirpoidea* var. *pseudoscirpoidea* is the most conspicuous associate in the eastern part of the region. Prominent lichens, occurring only in the western North Cascades, are *Cladonia gracilis* and *Cladonia mitis*. The moss *Polytrichum piliferum* and the lichens *Cetraria ericetorum*, *Cladonia pyxidata*, and *Thamnolia subuliformis* are prominent throughout the range (Table 1).

c) *Carex scirpoidea* var. *pseudoscirpoidea* community. In the eastern North Cascades (Fig. 10) this type is frequently found on dry, well drained slopes at all elevations and aspects. These sites become snowfree between mid-April and early May.

This community has an average of 35 species per stand and a total of 79. The dominant species, *Carex scirpoidea* var. *pseudoscirpoidea*, has a high mean cover (36%) and frequency (94%). This species is also one of the most common and abundant ones in a number of other alpine communities in the eastern North Cascades. *Potentilla diversifolia* var. *diversifolia*, *Carex phaeocephala*, *Festuca ovina* var. *brevifolia*, and *Arenaria obtusiloba* occur with moderate frequency and cover in the type. Prominent cryptogams are *Tortula ruralis*, *Bryum weigeli*, *Cetraria islandica*, and *Lecidea granulosa* (Table 1).

d) *Carex nardina* community. This community extends along the eastern flanks of the North Cascades (Fig. 10). It is restricted to the dry upper slopes of the higher peaks and shows no aspect preference. Winter snow cover is slight thus snowmelt is relatively early (late April to early May).

An average of 32 species per stand (70 in total) occur in this type. *Carex nardina*, with a high frequency of 94% and a moderately high cover of 19%, is the dominant plant. Common associates, although with low prominence throughout the community range, are *Festuca ovina* var. *brevifolia*, *Arenaria obtusiloba*, and *Smelowskia ovalis* (Table 1). In the southeastern part of the area (Star Peak) *Phlox hendersonii* is an abundant species. Important cryptogams are *Tortula ruralis*, *Thamnotia subuliformis*, and *Cornicularia aculeata*.

e) *Kobresia myosuroides* community. The *Kobresia*

myosuroides type occurs on high (above 2250 m elevation), well drained, moderately steep to steep, xeric upper slopes (Fig. 11) in the eastern part of the region (Fig. 10). These exposed habitats remain essentially snowfree most of the winter. Shallow snow accumulation is found only between the tufts of *Kobresia myosuroides* or among slight frost hummocks in the type.

Sixty-six species per stand (44 in total) are found in this community. *Kobresia myosuroides* is the major species with a high average cover (43%) and frequency (98%). Prominent associates are *Carex scirpoidea* var. *pseudoscirpoidea*, *Salix reticulata*, *Oxytropis campestris*, *Arenaria obtusiloba*, *Potentilla diversifolia* var. *diversifolia*, and *Solidago multiradiata*. The total cryptogam cover (63%) is the highest in the North Cascadian alpine. The most important of the many taxa are *Tortula ruralis*, *Polytrichum juniperinum*, *Cladonia pyxidata*, *Cetraria islandica*, *C. ericetorum*, and *C. cucullata*.

Blockfields

The level or gently sloping summits of almost every mountain in the North Cascades have accumulations of coarse rock detritus or "blockfields" (Embleton and King, 1971). Since most of these sites remain essentially snowfree all winter, frost has caused extensive breaking of the subjacent bedrock. Other frost associated phenomena, such as sorted and unsorted circles and nets (Washburn, 1956) on level surfaces and unsorted stripes (Washburn, 1956) or

Figure 11. A *Kobresia myosuroides* community at 2400 m on Arnold Peak, Washington. *Salix reticulata*, *Oxytropis campestris*, and *Arenaria obtusiloba* are the most prominent plants occurring between the *Kobresia* clumps.



vegetation stripes on slopes, are common to the blockfields.

The blockfields in the North Cascades can arbitrarily be separated into four general groups (herbfields, vegetation stripes, boulderfields, and fellfields) based on amount or arrangement of vegetative cover or size of rock detritus. If total vegetative cover is greater than 50% the term herbfield is used. Vegetation stripes, where the vegetation is arranged in long parallel strips, 1 to 2 m apart, are a second group. If rock or boulder cover comprises at least 50% of the ground cover the term boulderfield is appropriate. If none of the above criteria are met the site is then classified as fellfield.

Thirty-nine blockfield stands, containing a total of 94 vascular plants and 38 cryptogams, were sampled and analyzed. *Beta* diversity (Whittaker, 1960) was so great in these stands that most of them plotted in a single, undecipherable group in the center of ordinations. Separation of the stands into the above four classes (*i.e.*, fellfields, herbfields, etc.) or into major geographic regions did not improve ordination performance. Use of several cluster techniques (Pritchard and Anderson, 1971) illustrated stand relationships more clearly and verified that *beta* diversity was extremely high. The cluster techniques indicated that no fewer than 24 sets could be recognized within the 39 sampled stands. These sets had little, or no, correlation with amount of plant or rock cover and revealed no regional pattern.

The blockfield stands throughout the North Cascades have many major species in common (Table 2). This large number of common species and their relatively low constancy and varying abundance results in a continuous vegetational change within which no divisions can be satisfactorily made, at least within the community concept used in this study. It is quite likely that, with more intensive sampling, reduced plot size, and the inclusion of all cryptogams, a "community" pattern would emerge, at least from the fellfields and boulderfields. These stands would probably be recognizeable at a micro-community level and would correspond to microhabitats within the fellfields or boulderfields.

In general, the most notable floristic differences within the blockfields are due to those species having restricted tolerance ranges or geographic distributions in the North Cascades. A number of species (e.g., *Solidago multiradiata*, *Oxytropis campestris* var. *gracilis*, *Achillea millefolium* var. *alpicola*, and *Cerastium arvense*, although found in a number of communities throughout the region, occur only in blockfields of the western North Cascades. Many species reach their geographical distribution limits in the North Cascades. *Phlox hendersonii* extends north only to the extreme southeastern part of the study area (Star Peak), where it is an important blockfield component. Less important species occurring with the latter, and having a similar northern range limit, are *Eritrichum nanum* and

TABLE 2. Mean prominence values and constancy of the major plant species in blockfield stands of four areas in the North Cascades. a,b

Species	Northwest (15)			Northcentral (9)			Southeast (9)			Northeast (5)		
	PVC	C		PV	C		PV	C		PV	C	
<i>Phlox diffusa</i>	63	80		24	66		5	22				
<i>Potentilla diversifolia</i>	49	53		9	77		12	22		16	80	
var. <i>diversifolia</i>	40	67										
<i>Solidago multiradiata</i>												
<i>Oxytropis compestris</i>	40	47										
var. <i>gracilis</i>	21	33		4	33					T	20	
<i>Carex albonigra</i>												
<i>Achillea millefolium</i>	17	33										
var. <i>alpicola</i>	16	53										
<i>Cerastium arvense</i>	15	47		32	66					12	60	
<i>Selaginella densa</i>	14	53		14	88		25	88		20	60	
<i>Carex phaeocephala</i>	14	47					P	11		T	20	
<i>Poa alpina</i>												
<i>Festuca ovina</i>	13	88		7	88		19	88		22	100	
var. <i>brevifolia</i>	11	53		T	22					43	100	
<i>Silene acaulis</i>												
<i>Lupinus lepidus</i>	3	53		2	22		53	100		65	40	
var. <i>lobbii</i>												
<i>Sedum lanceolatum</i>												
var. <i>lanceolatum</i>	3	40		4	88		18	100		7	60	
<i>Luzula spicata</i>	2	40		4	66		9	100		16	100	
<i>Antennaria alpina</i>	2	27		3	66		12	77		18	80	
<i>Trisetum spicatum</i>	1	47		T	66		10	88		7	100	
<i>Erigeron compositus</i>												
var. <i>glabratus</i>	1	7		3	55		8	33		12	100	

TABLE 2. Continued.

Species	Northwest (15)		Northcentral (9)		Southeast (9)		Northeast (5)	
	PVC	C	PV	C	PV	C	PV	C
<i>Penstemon procerus</i>	T	20	T	11	27	77	T	20
<i>Draba incerta</i>	T	14	T	22	11	55	T	20
<i>Arenaria obtusiloba</i>	T	13	10	77	40	66	53	100
<i>Arenaria capillaris</i>			13	44	53	66	3	80
<i>Erigeron aureus</i>			5	55	14	88	16	60
<i>Carex nardina</i>			4	33	15	77		
<i>Phlox hendersonii</i>					72	77		
<i>Carex scopulorum</i>					19	22	20	100
<i>Carex scirpoides</i>								
var. <i>pseudoscirpoides</i>								

^aNumber of stands sampled are enclosed in parentheses.

^bOnly species with a prominence value of 10, or more, in at least one area are included in this table.

^cAbbreviations: PV - prominence value, C - constancy.

Douglasia nivalis. Farther west, in the Glacier Peak area, *Collomia debilis* var. *larsenii* reaches its northern limits and is often abundant in blockfields. Rocky Mountain or arctic elements, extending into only the northcentral or northeastern part of the North Cascades are *Carex scirpoidea* var. *pseudoscirpoidea*, *Potentilla nivea*, and *P. uniflora*.

Krummholz stands

The overstory composition of krummholz stands changes markedly from west to east in the North Cascades. On the west side of the range *Abies lasiocarpa* (Hook.) Nutt. is the dominant overstory species. *Tsuga mertensiana* and *Chamaecyparis nootkatensis* occur infrequently and rare occurrences of *Abies amabilis* were noted. In the central North Cascades *Abies lasiocarpa*, *Picea engelmannii*, and *Larix lyallii* Parl. are common. The latter is occasionally found in a prostrate form, but more often is erect, with flagged tops, and grows adjacent to the more prostrate conifers. *Pinus albicaulis* also occurs in the central North Cascades but is less frequent than the previous species. On the east side of the range *Abies lasiocarpa* and *Larix lyallii* decrease in abundance while *Picea engelmannii* and *Pinus albicaulis* are common.

The understory of the 42 krummholz stands sampled during the study showed low cover and considerable variation in composition (Table 3). The use of ordination and cluster techniques failed to correlate understory composition with either overstory composition or geographical region. The

TABLE 3. Mean prominence values of plant species in four krummholz types in three regions
(west, central, and east) of the North Cascades Range.

Species	Krummholz Dominants							
	<i>Abies lasiocarpa</i>		<i>Larix lyallii</i>		<i>Picea engelmannii</i>		<i>Pinus albicaulis</i>	
	West (6)	Central (3)	Central (5)	East (2)	Central (4)	East (5)	Central (3)	East (11)
CONIFERS								
<i>Abies lasiocarpa</i>	950	885	—	—	—	—	—	3
<i>Pinus albicaulis</i>	—	10	—	—	—	1	869	834
<i>Picea engelmannii</i>	—	7	—	—	850	963	1	T
<i>Larix lyallii</i>	—	—	740	975	—	—	—	—
VASCULAR PLANTS								
<i>Phyllodoce glanduliflora</i>	68	—	—	—	—	18	—	90
<i>Carex spectabilis</i>	61	—	—	—	—	—	—	—
<i>Vaccinium deliciosum</i>	53	—	—	—	—	—	—	—
<i>Phyllodoce empetriformis</i>	42	—	6	—	—	—	—	—
<i>Leutkea pectinata</i>	40	3	45	—	—	—	—	—
<i>Cassiope mertensiana</i>	12	103	340	—	—	—	—	—
<i>Empetrum nigrum</i>	8	—	—	—	—	—	—	—
<i>Arnica latifolia</i>								
var. <i>gracilis</i>	5	—	—	—	—	—	—	—
<i>Festuca ovina</i>								
var. <i>brevistyla</i>	5	—	—	9	1	6	1	9
<i>Polygonum bistortoides</i>	4	—	—	—	—	—	—	—
<i>Solidago multinodiata</i>	4	—	—	—	—	—	—	—
<i>Deschampsia atropurpurea</i>	3	—	—	—	—	—	—	63

TABLE 3. Continued.

Species	Krummholz Dominants									
	<i>Abies lasiocarpa</i>		<i>Larix lyallii</i>		<i>Picea engelmannii</i>		<i>Pinus albicaulis</i>			
	West (6)	Central (3)	Central (5)	East (2)	Central (4)	East (5)	Central (3)	East (11)		
<i>Lupinus latifolius</i>	3	—	—	—	—	—	—	—	—	—
<i>var. subalpinus</i>	2	9	8	—	1	—	—	—	—	—
<i>Hieracium gracile</i>	2	—	—	—	—	—	—	—	—	—
<i>Potentilla flabellifolia</i>	2	—	—	—	—	—	—	—	—	—
<i>Lycopodium sitchensis</i>	2	—	—	—	—	—	—	—	—	—
<i>Salix cascadenis</i>	2	—	—	2	—	—	—	—	—	—
<i>Polygonum viviparum</i>	2	—	—	—	—	—	—	—	—	—
<i>Campanula rotundifolia</i>	1	—	—	—	—	—	—	—	—	—
<i>Potentilla diversifolia</i>	1	—	—	2	—	1	—	5	—	—
<i>Luzula wahlenbergii</i>	1	—	101	—	—	—	—	—	—	—
<i>Veronica wormsjoldii</i>	1	4	6	—	—	—	—	—	—	—
<i>Erigeron peregrinus</i>	1	—	—	—	—	—	—	—	—	—
<i>Achillea millefolium</i>	1	—	—	—	—	—	—	—	—	—
<i>Silene parryi</i>	1	—	—	—	—	—	—	—	—	—
<i>Antennaria alpina</i>	1	—	—	—	—	—	1	1	—	—
<i>Vaccinium scoparium</i>	—	158	24	—	100	2	—	26	—	—
<i>Penstemon davidsonii</i>	—	—	—	24	—	4	4	35	—	—
<i>var. davidsonii</i>	—	11	—	—	1	—	—	—	—	—
<i>Pedicularis racemosa</i>	—	10	—	—	—	—	—	—	—	—
<i>Poa sandbergii</i>	—	6	5	—	4	—	—	—	—	—
<i>Erigeron aureus</i>	—	6	—	—	8	7	1	7	—	—
<i>Arenaria capillaris</i>	—	6	9	—	3	2	—	1	—	—
<i>Haplopappus lyallii</i>	—	5	12	4	1	4	7	6	—	—
<i>Selagenella densa</i>	—	4	—	—	1	1	—	1	—	—
<i>Phlox hendersonii</i>	—	3	—	—	4	—	7	—	—	—

TABLE 3. Continued.

Species	Krummholz Dominants							
	<i>Abies lasiocarpa</i>		<i>Larix lyallii</i>		<i>Picea engelmannii</i>		<i>Pinus albicaulis</i>	
	West (6)	Central (3)	Central (5)	East (2)	Central (4)	East (5)	Central (3)	East (11)
<i>Anenome drummondii</i>	—	3	1	—	10	—	7	—
var. <i>drummondii</i>	—	3	3	—	1	—	—	1
<i>Sedum lanceolata</i>	—	1	—	—	—	—	—	T
<i>Antennaria lanata</i>	—	1	—	—	—	—	—	—
<i>Castilleja parviflora</i>	—	—	58	—	—	—	—	T
<i>Penstemon procerus</i>	—	—	19	—	4	2	—	1
<i>Poa nervosa</i>	—	—	11	—	2	—	—	—
<i>Phlox diffusa</i>	—	—	5	—	—	—	—	T
<i>Agoseris glauca</i>	—	—	3	—	—	—	—	—
<i>Senecio streptanthifolius</i>	—	—	—	—	—	—	—	—
<i>Arenaria obtusiloba</i>	—	—	—	33	1	3	—	1
<i>Draba incerta</i>	—	—	—	4	—	—	—	T
<i>Dryas octapetala</i>	—	—	—	4	—	24	—	14
<i>Carex scirpoidea</i>	—	—	—	—	—	—	—	—
var. <i>pseudoscirpoidea</i>	—	—	—	2	—	—	—	T
<i>Juniperus communis</i>	—	—	—	2	—	2	199	42
<i>Carex phaeocephala</i>	—	—	—	2	1	5	1	2
<i>Polemonium pulcherrimum</i>	—	—	—	2	1	1	—	—
var. <i>pulcherrimum</i>	—	—	—	—	1	—	—	—
<i>Poa alpina</i>	—	—	—	—	1	—	—	—
<i>Juncus parryi</i>	—	—	—	—	1	—	—	—
<i>Ledum groenlandicum</i>	—	—	—	—	12	—	—	—
<i>Carex rossi</i>	—	—	—	—	8	—	—	—
<i>Lupinus lepidius</i>	—	—	—	—	2	—	1	—

sparse understory flora appeared to be selected from nearby communities irrespective of the community type. Regional separation is not consistent since species such as *Phyllodoce glanduliflora* and *Festuca ovina* var. *brevistyla* may be important across the entire range (Table 3). *Carex concinnoides* and *Ledum groenlandicum* are the only species essentially restricted to krummholz stands in the alpine zone of the North Cascade. *Vaccinium scoparium* is the only species that reaches its maximum prominence beneath krummholz stands.

Plant Diversity

Alpha diversity measurements (Whittaker, 1970; 1972) included species richness or number of species in the sample (S), general diversity or richness and dominance concentration (\bar{H}), and equitability or evenness (E). Trends of S , \bar{H} , and for the most part, E are similar (Fig. 12). Although the communities or vegetative units, along the abscissas of Fig. 12, have been placed arbitrarily they do represent a reasonable gradient (based on both quantitative and qualitative data) from "mild" to "harsh" environments. Communities with relatively late snowmelt, adequate summer soil moisture, high leaf water potentials, and low degree of exposure (e.g., snowbed communities in the western and central North Cascades, heath communities and krummholz stands) have low S , \bar{H} , and E values and are considered mild environments. These communities are also those in which most of the lower elevation (mainly subalpine) species

occur, thus indicating a milder or more favorable environment. The diversity values tend to increase with earlier snowmelt, drier soils, lower leaf water potentials and greater exposure. The latter conditions represent a more "harsh" environment and are typical of dry sedge and dry grass communities, herbfields and vegetation stripes. With a continued increase in harshness a point is reached at which *S* and *H* begin to decline. These lower values are attained in the fellfield, boulderfield, and unstable snow-bed sites. On these more rigorous sites *E* declines only slightly.

Although the epipetric and epiphytic mosses were not included in this study, they are of importance only in fellfields, boulderfields, streamsides, and rock outcrops. Their effect on *alpha* diversity components in fellfields and boulderfields would be slight since they are usually few in number and of low abundance, due to frequent disturbance of the surface strata. In several instances, however, *Umbilicaria*, *Lecanora*, or *Lecidea* sp. were of high cover, thus the equitability component would be lower than that shown in Fig. 12.

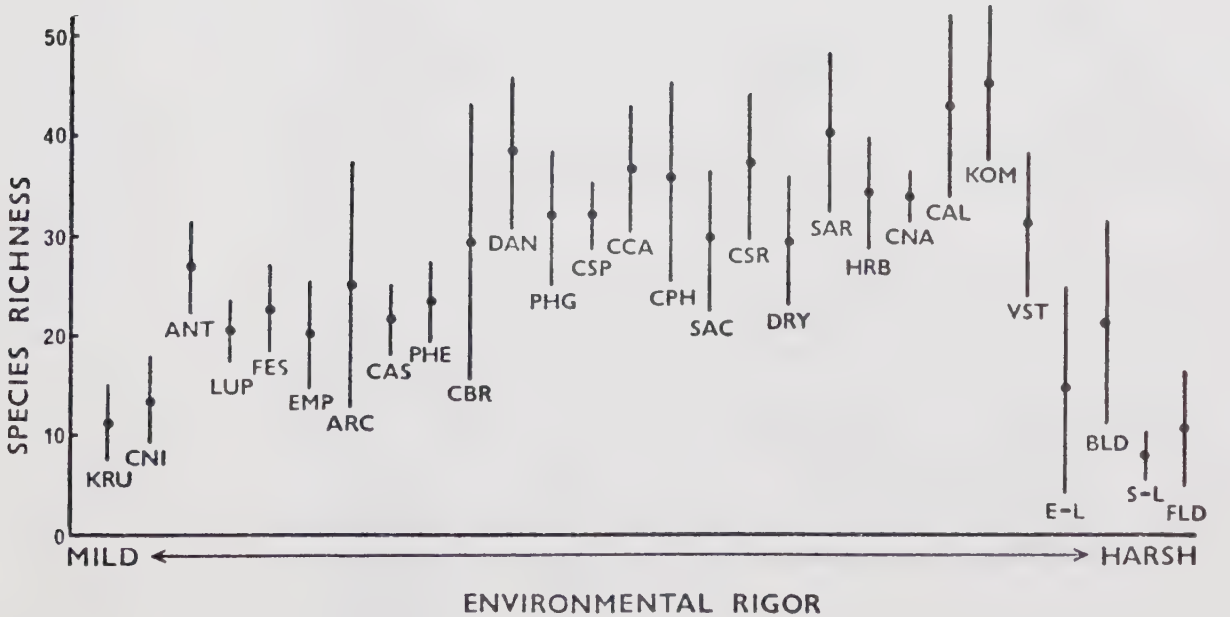
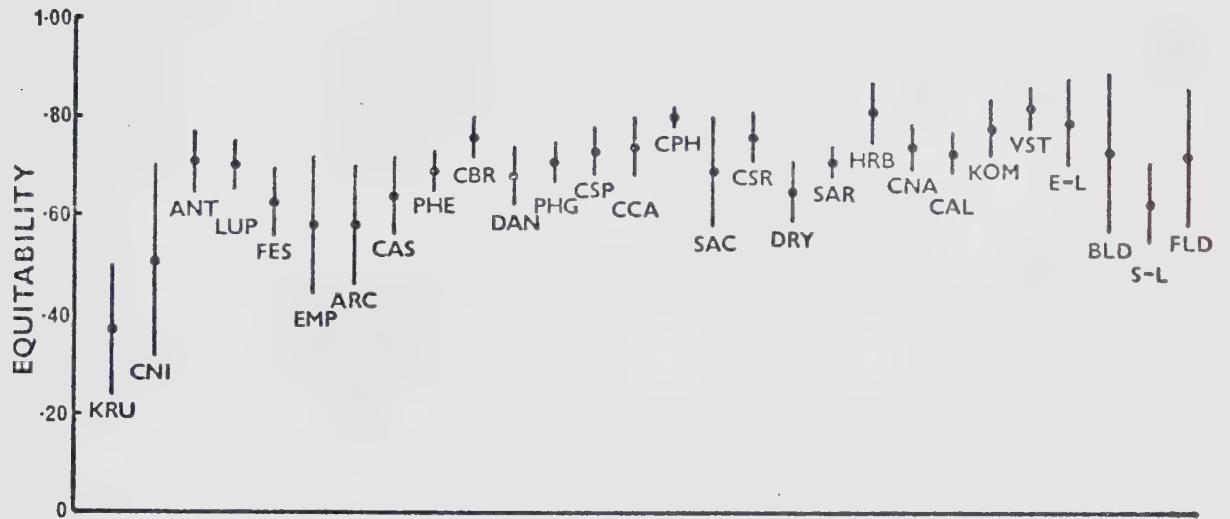
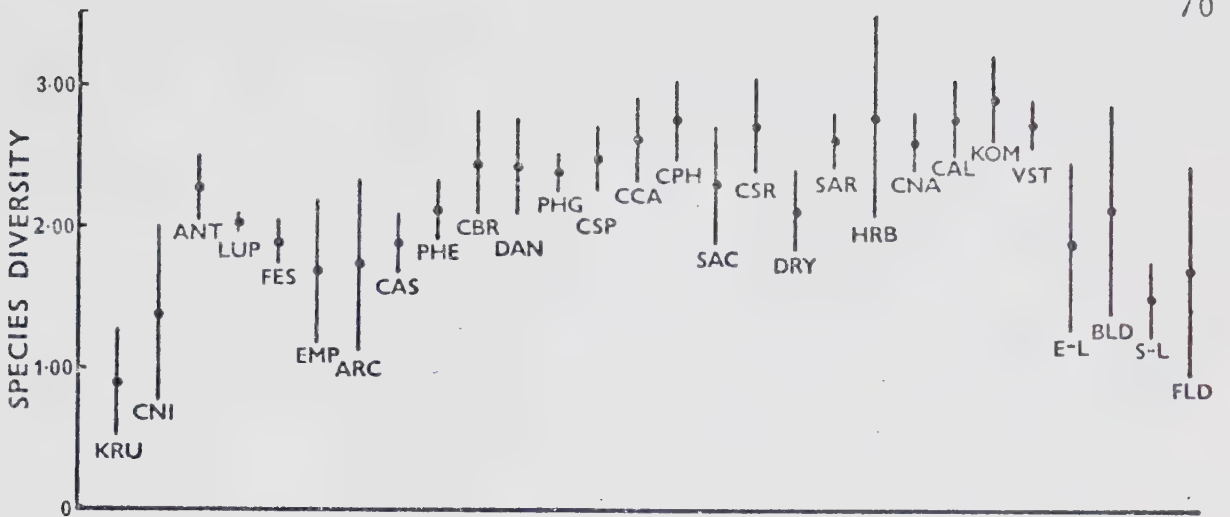
Soils

Morphology

Alpine soils are relatively poorly developed and fall within the Spodosol, Inceptisol, and Entisol Orders. All but the latter have developed in parent materials that contain a high pyroclastic component. These pyroclastic

Figure 12. Means and standard deviations (vertical lines) of general diversity, equitability, and species richness in relation to environmental rigor.

Abbreviations: S-L - *Saxifraga tolmiei*-*Luzula wahlenbergii*, E-L - *Eriogonum pyrolaeifolium*-*Luzula wahlenbergii*, CNI - *Carex nigricans*, ANT - *Antennaria lanata*, CBR - *Carex breweri*, CCA - *Carex capitata*, LUP - *Lupinus latifolius*, FES - *Festuca viridula*, CAS - *Cassiope mertensiana*, PHE - *Phyllodoce empetrifolia*, PHG - *Phyllodoce glanduliflora*, ARC - *Arctostaphylos uva-ursi*, EMP - *Empetrum nigrum*, SAR - *Salix reticulata*, SAC - *Salix cascadiensis*, DRY - *Dryas octopetala*, DAN - *Danthonia intermedia*, CAL - *Calamagrostis purpurascens*, CSP - *Carex spectabilis*, CPH - *Carex phaeocephala*, CSR - *Carex scirpoidea* var. *pseudoscirpoidea*, CNA - *Carex nardina*, KOM - *Kobresia myosuroides*, KRU - Krummholz, HRB - Herbfield, VST - Vegetation stripes, FLD - Fellfield, BLD - Boulderfield.



deposits originated from a number of recent volcanic eruptions within, and to the south of, the study area (Bockheim, 1972; van Ryswyk, 1969).

The Spodosols of the region occur mainly beneath krummholz and heath vegetation. The best development occurs beneath krummholz, especially in the western North Cascades. These profiles have moderately thick (up to 7 cm) organic layers, moderately well developed eluvial horizons, and illuvial horizons characterized by high organic matter content. The following profile (10) is typical of krummholz stands in the western North Cascades:

Horizon	Description
O1	7 to 1 cm; fresh coniferous (krummholz) litter.
O2	1 to 0 cm; partially humified forest litter.
A2	0 to 7 cm; dark reddish gray (10 R 3/1) sandy loam; weak, medium subangular blocky structure; breaking down to moderate fine crumb; very friable; abundant fine to medium roots; extremely acid (pH 4.0); abrupt, wavy boundary.
B21	7 to 19 cm; dark reddish brown (2.5 YR 2/4) loam; weak, medium subangular blocky structure, breaking down to moderate, fine crumb; friable; abundant fine to medium roots; extremely acid (pH 4.3); abrupt, smooth boundary.

Horizon	Description
B22	19 to 44 cm; dark brown (7.5 YR 3/2) very gravelly loam; weak, very fine crumb structure; friable; few fine roots; very strongly acid (pH 4.6); abrupt, irregular boundary.
R	44 to 55 cm +; weathered shale.

Spodosols associated with heath vegetation are characterized by thin organic horizons (1 cm), absent or imperceptible albic horizons, and abundant organic matter in the illuvial horizons. Profile 9 is typical of heath communities in the western North Cascades. Detailed analysis of this profile by Bockheim (1972) showed that in the B2 horizon the ratio of percent pyrophosphate-extractable Fe + Al to percent dithionite-extractable Fe + Al exceeds 0.5, thus placing it within the Spodosol Order.

Horizon	Description
01	Trace, fresh plant litter (mainly heath species).
02	1 to 0 cm; partially humified herbaceous plant litter.
A1	0 to 8 cm; dark reddish brown (5 YR 3/3) fine sandy loam; moderate, fine crumb structure; very friable; abundant very fine to medium roots; extremely acid (pH 4.3); clear, smooth boundary.

Horizon	Description
B21	8 to 16 cm; dark yellowish brown (10 YR 3/4) fine sandy loam; moderate, fine crumb structure; friable; abundant fine to medium roots; very strongly acid (pH 5.0); gradual, smooth boundary.
B22	16 to 37 cm; dark yellowish brown (10 YR 4/4) gravelly sandy loam; weak to moderate, fine crumb structure; friable; plentiful very fine to fine roots; very strongly acid (pH 4.9); abrupt, smooth boundary.
C	37 to 66 cm +; yellowish brown (10 YR 5/4) very gravelly sandy loam; massive; friable; few to plentiful fine roots; very strong acid (pH 4.8).

Most of the communities in the North Cascades have soils typical of the Inceptisol Order. The Inceptisols are rather weakly developed, lacking significant illuviation, eluviation, or extreme weathering. These soils have moderately thick (4 to 10 cm) turfy A horizons and relatively high accumulations of organic matter in the illuvial horizons. Communities associated with the Inceptisols range from the poorly drained snowbed types to the well drained dry grass and dry sedge types.

Inceptisols in poorly drained depressions often have one, or more, ash layers present. Buried A horizons may also occur below these ash layers. Profile 28 illustrates

the characteristics of these soils in a *Carex nigricans* community in the central North Cascades.

Horizon	Description
O1	Trace; fresh sedge (<i>Carex nigricans</i>) litter.
O2	2 to 0 cm; partially humified sedge litter.
A1	0 to 5 cm; very dark grayish brown (10 YR 3/2) loam; weak, fine crumb structure; friable; abundant very fine roots; very strongly acid (pH 4.7); abrupt, wavy boundary.
B21	5 to 11 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; friable; plentiful very fine roots; strongly acid (pH 5.2); gradual, smooth boundary.
B22	11 to 21 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; friable; plentiful very fine roots; strongly acid (pH 5.5); abrupt, wavy boundary.
C1	21 to 24 cm; grayish brown (10 YR 5/2); sandy loam; weak, fine crumb structure; few very fine roots; strongly acid (pH 5.5); abrupt, wavy boundary.
C2	24 to 28 cm; dark yellowish brown (10 YR 4/4) sandy clay loam; weak, fine crumb structure; few very fine roots; strongly acid (pH 5.5); abrupt, wavy boundary.
C3	28 to 31 cm; brown (10 YR 4/3) sandy loam; weak, fine crumb structure; few very fine

Horizon	Description
	roots; strongly acid (pH 5.5); abrupt, wavy boundary.
C4	31 to 34 cm; dark brown (10 YR 3/3) sandy loam; weak, fine crumb structure; few very fine roots; strongly acid (pH 5.4); abrupt, wavy boundary.
C5	34 to 60 cm +; dark yellowish brown (10 YR 3/4) sandy loam; weak, fine crumb structure; few very fine roots; strongly acid (pH 5.2).

Well drained sites have A-B-C profiles typical of the Inceptisols. The following profile (27) occurred beneath a *Kobresia myosuroides* community in the eastern North Cascades:

Horizon	Description
O1	3 to 2 cm; fresh sedge litter.
O2	2 to 0 cm; partially humified sedge litter.
A1	0 to 9 cm; black (10 YR 2/1) sandy loam; weak, fine crumb structure; friable; abundant, very fine to fine roots; strongly acid (pH 5.3); gradual, wavy boundary.
B21	9 to 19 cm; very dark brown (10 YR 2/2) sandy loam; weak, fine crumb structure; friable; plentiful, very fine roots; medium acid (pH 5.7); abrupt, wavy boundary.
B22	19 to 24 cm; dark yellowish brown (10 YR 3/4)

Horizon	Description
	sandy loam; weak, very fine crumb structure; friable; few very fine roots; medium acid (pH 5.7); abrupt, irregular boundary.
C	24 to 60 cm +; brown (10 YR 4/3) gravelly sandy loam; weak, fine crumb structure; friable; few very fine roots; medium acid (pH 5.8).

The most poorly developed soils in the region are the Entisols. These soils are associated with either unstable snowbed sites or the high windswept ridges and plateaus. The latter areas usually support blockfield vegetation although several of the shrub community types may also occur on these sites. The Entisols generally have only thin surficial A horizons beneath the sparse vegetative cover. Profile 7 is typical of the Entisols occurring in the blockfields of the western North Cascades.

Horizon	Description
C1	0 to 2 cm; very dark gray (5 Y 3/1) gravelly loam; structureless; friable; no roots; very strongly acid (pH 4.7); gradual, smooth boundary.
C2	2 to 18 cm; very dark grayish brown (2.5 Y 3/2) gravelly sandy loam; structureless; friable; no roots; very strongly acid (pH 4.6); abrupt, wavy boundary.

Horizon	Description
R	18 cm +; weathered shale.

Physical and chemical properties

Physical and chemical properties of soil profiles were determined in a number of the major plant communities across the North Cascades Range (Table 4). Soil pH varies markedly both within and between soil profiles, but generally decreases with depth. The most acid (pH 3.8 to 5.0) are those associated with krummholz and heath vegetation in the western North Cascades. Inceptisols are also highly acid (pH 3.9 to 5.1) in the western part of the region. Less acid (pH 4.7 to 5.9) soils occur in snowbed and fellfield habitats throughout the range. The least acid (pH 5.2 to 6.0) soils are those associated with *Dryas octopetala*, dry grass, and dry sedge communities in the eastern North Cascades.

All soils become coarser textured with depth. Total sand generally increases with depth. Maximum clay concentrations usually occur in the upper B horizon. Sand plus silt to clay ratios are relatively high in all soils, possibly a reflection of the large amounts of pyroclastic materials present.

Organic matter is highest in the surface mineral horizons (except A2 horizons) and decreases with depth in the western North Cascades. Farther east organic matter levels are lower and maximum organic matter concentration often occurs in the upper B2 horizons.

TABLE 4. Continued

Community	Profile	Horizon	pH	Texture			Organic matter (%)	Available			Exchangeable cations (me/100 g)				TEC (me/100 g)
				Sand (%)	Silt (%)	Clay (%)		N (ppm)	P (ppm)	K (ppm)	Na	K	Ca	Mg	
<i>Antennaria lanata</i>	29	A1	4.7	61.4	21.9	16.7	10.2	1.0	14.0	217.5	0.01	0.65	0.28	0.25	27.1
		B21	5.3	60.7	23.2	16.1	12.1	0.0	5.0	87.5	0.01	0.35	0.28	0.00	32.2
		C	5.4	--	--	--	--	--	--	--	--	--	--	--	--
<i>Festuca viridula</i>	30	A1	4.9	62.4	21.9	15.7	5.8	0.5	14.5	77.5	0.01	0.17	0.25	0.12	19.6
		B21	5.3	60.3	22.7	17.0	8.4	0.5	5.5	60.0	0.00	0.13	0.50	0.00	23.8
		C	5.4	53.3	31.3	15.4	--	--	--	--	--	--	--	--	--
<i>Carex capitata</i>	25	A1	4.9	54.1	33.7	12.2	10.9	0.0	12.5	55.0	0.01	0.20	1.50	0.29	26.9
		B21	5.6	54.4	29.2	16.4	5.3	0.0	4.5	45.0	0.05	0.08	0.25	0.08	15.0
		C	5.9	68.1	15.0	16.9	--	--	--	--	--	--	--	--	--
<i>Dryas octopetala</i>	26	A1	5.2	61.2	21.6	17.2	1.0	0.0	9.5	37.5	0.02	0.06	0.70	0.16	11.1
		B21	5.7	61.4	23.5	15.1	0.6	0.0	17.5	45.0	0.01	0.06	0.25	0.04	6.9
		C	5.8	54.3	31.4	14.3	--	--	--	--	--	--	--	--	--
<i>Carex nardina</i>	24	A1	5.7	60.1	23.9	16.0	8.4	0.0	10.0	110.0	0.10	0.27	2.88	0.49	15.5
		B21	5.7	60.8	22.4	16.8	9.1	0.0	1.0	82.5	0.05	0.17	1.63	0.29	16.5
		B22	5.8	58.1	24.2	17.7	1.4	0.0	10.5	65.0	0.02	0.09	0.50	0.04	10.1
		C	6.0	54.0	31.1	14.9	--	--	--	--	--	--	--	--	--
<i>Kobresia myosuroides</i>	27	A1	5.3	61.8	21.0	17.2	9.2	0.5	9.5	72.5	0.27	0.18	2.25	0.29	17.2
		B21	5.7	57.1	23.1	19.8	9.4	0.0	0.0	42.5	0.02	0.09	1.00	0.00	18.7
		B22	5.7	57.4	25.1	17.5	--	--	--	--	--	--	--	--	--
		C	5.8	55.1	29.7	15.2	--	--	--	--	--	--	--	--	--

^aTexture and organic matter for profiles 9 and 10 from Bockheim (1972).

Total exchange capacity levels are positively correlated with the organic matter trends. Exchangeable cations in soil profiles of the region generally decrease with depth. Sodium occurs only in small quantities, except in the A2 horizons of krummholz stands and A1 horizons of *Kobresia bellardii* communities. Calcium, magnesium, and potassium levels are low, but are comparable to those determined on similar parent materials in other alpine areas (Klickoff, 1965; Nimlos and McConnell, 1965; Bliss, 1966; Johnson, 1970). In the eastern North Cascades (British Columbia) van Ryswyk (1969) found much higher sodium and slightly higher calcium levels in alpine soils.

Available phosphorus generally decreases with depth in contrast to some alpine soils which increase (Nimlos and McConnell, 1965). Kuramoto and Bliss (1970) also found phosphorus decreased with depth in the Olympic Mountains, Washington. Potassium levels also decrease with depth and have their highest levels (162.5 to 217.5 meq/100 g) in *Carex nigricans* and *Antennaria lanata* snowbed communities. Available nitrogen levels are low throughout the region. Nimlos *et al.* (1965) also reported low nitrate-nitrogen levels in alpine soils in Montana, although "total" nitrogen was high. In the eastern North Cascades van Ryswyk (1969) reported low nitrogen values while in the western North Cascades Bockheim (1972) reported higher nitrogen values.

Mesoclimate

Precipitation

Long-range climatic data for the few permanent weather stations show a decreasing summer rainfall pattern from west to east (U.S. Weather Bureau, no dates). This pattern may be broken during individual summers, such as 1972 when precipitation on Chopaka Mountain (east) exceeded that on Grouse Ridge (west) (Table 5). Length of the intervals between rainfall fluctuates greatly. The summer of 1970 was characterized by frequent storms while lengthy periods without precipitation occurred during the summers of 1971 and 1972.

Temperature

The long-term summer temperature patterns show higher temperatures in the eastern Cascades and lower temperatures in the western Cascades (U.S. Weather Bureau, no dates). During 1970, when storm frequency was high, temperature varied greatly. Periods of continuous, relatively high temperatures were common during 1971 and 1972. Highs of 26.7 to 28.3°C were reached in the last week of July 1971 and the first week of August 1972 on Grouse Ridge. The highest temperatures (30.6°C) recorded on Slate Peak occurred during the last week of July 1971. At the Chopaka Mountain weather station highs of 32.2 to 35.6°C were attained in the first week of August 1972. Temperatures below 0°C may occur at any time during the summer, although lows of 5 to

TABLE 5. Environmental data for five weather stations in the North Cascades Range.

Date	Station ^a	Solar radiation (langley/ day) 15 cm	Temperature (°C)			Wind (m/sec) 60 cm	VPD (cm Hg) 15 cm	Precip- itation (cm) 60 cm
			Mean daily minimum	Mean daily	Mean daily maximum			
1970								
6/13-7/5 ^b	Grouse	515	6.8	12.2	16.9	1.9	.09	2.57
7/6-8/2	Grouse	484	6.1	11.0	15.9	1.4	.12	8.39
8/3-8/29 ^c	Grouse	475	6.7	11.2	15.8	1.4	.12	1.65
1971								
6/30-8/1 ^d	Grouse	567	4.8	10.3	15.8	1.7	.12	2.67
8/2-8/30	Grouse	528	6.2	11.3	17.1	2.0	.10	2.20
1972								
6/30-7/30 ^e	Grouse	-	5.8	11.8	17.5	2.0	.11	8.07
8/7-8/22	Grouse	-	5.5	10.2	16.4	-	.11	-
1971								
7/21-7/29	Slate	-	11.5	17.9	25.2	2.8	.17	0.00
7/30-9/3 ^f	Slate	641	7.2	13.1	19.8	2.9	.14	3.31
1972								
7/23-8/15 ^g	Slate	734	6.4	12.6	20.6	2.3	-	3.07
1970								
8/6-8/30	Sourdough	-	2.8	9.4	18.0	-	.10	0.54
8/31-9/13	Sourdough	-	-	-	-	-	-	5.25
1970								
7/4-7/30	Sahale	-	-	-	-	4.5	-	8.76
7/31-8/30	Sahale	-	-	-	-	4.2	-	2.27

TABLE 5. Continued.

Date	Station	Solar radiation (langley/day) 15 cm	Temperature (°C)			Wind (m/sec) 60 cm	VPD (cm Hg) 15 cm	Precipitation (cm) 60 cm
			Mean daily minimum	Mean daily maximum	Mean daily maximum			
1972								
6/6-6/25 ^h	Chopaka	773	0.1	2.7	6.3	-	.03	11.05
6/26-7/16 ⁱ	Chopaka	-	1.0	5.7	11.1	3.7	.08	1.06
7/17-8/16 ⁱ	Chopaka	573	6.5	14.0	23.5	3.2	.24	5.27

^a Weather station locations appear on Figure 1.

^b Temperature, VPD, and solar radiation based on 18, 18, and 13 days data, respectively.

^c Temperature and VPD based on 19 days data.

^d Temperature, VPD, and solar radiation based on 24, 21, and 20 days data, respectively.

^e Temperature and VPD based on 22 days data.

^f Solar radiation based on 18 days data.

^g VPD and solar radiation based on 13 and 9 days data, respectively.

^h Solar radiation based on 7 days data.

ⁱ VPD and solar radiation based on 20 and 10 days data, respectively.

10°C are most common.

Atmospheric moisture

Average vapor-pressure deficits (VPD) are relatively low across the entire North Cascades Range (Table 5). Maximum VPD at Grouse Ridge during the three summers of this study was 0.58 cm Hg on June 20, 1970. At Slate Peak VPD reached 0.90 and 0.88 cm Hg on July 30 and 31, 1971. The highest VPD (1.15 cm Hg) recorded during the study occurred on Chopaka Mountain on August 5, 1972. In general, the data indicate that evaporation is highest in the eastern Cascades and lowest in the western Cascades.

Solar radiation

Summer solar radiation patterns fluctuate markedly from year to year in the North Cascades. In general, average recorded values increase from west to east (Table 5) due to the increased cloudiness in the western North Cascades. The highest recorded value (818 langleys/day) occurred several times during 1972 on Chopaka Mountain. In the central North Cascades (Slate Peak) a high of 762 langleys/day was reached on August 5, 1971 and on several occasions during 1972 highs of 755 to 760 langleys/day were reached. At Grouse Ridge highs were typically between 660 and 680 langleys/day although 790 langleys/day was recorded on July 7, 1971.

Wind

Wind speeds are lower in the western North Cascades

and slightly higher in the central and eastern North Cascades (Table 5). Maximum average velocity (2.4 m/sec) at Grouse Ridge occurred during a 24-hour stormy period in early August 1971. Average maximum velocities at Sahale Mountain were the highest (5.3 m/sec over 7 days during mid-August 1970) during the study period but this is likely due to its ridgetop location at the headwaters of two large drainage systems. The average maximum velocities reached at Slate Peak and Chopaka Mountain were 3.0 and 4.5 m/sec respectively, during 1972. Wind speeds in the eastern North Cascades and on exposed ridges in the central North Cascades (e.g., Sahale Mountain) are comparable to those recorded on Mt. Washington, New Hampshire (Bliss, 1966) and the Olympic Mountains, Washington (Bliss, 1969).

Environmental Gradient

Vegetation

An alpine slope at 1790 m elevation on Grouse Ridge, Mt. Baker, was selected for an intensive environmental gradient study. This slope provided an opportunity to study the responses of plant species to an environmental gradient in a region where abrupt topographic discontinuities usually result in a mosaic of segregated plant community types (Fig. 13). The changes in species composition and structure along this continuum are, for the most part, gradual (Table 6, Figs. 14 and 15).

At the top of the ridge, where the slope angle is

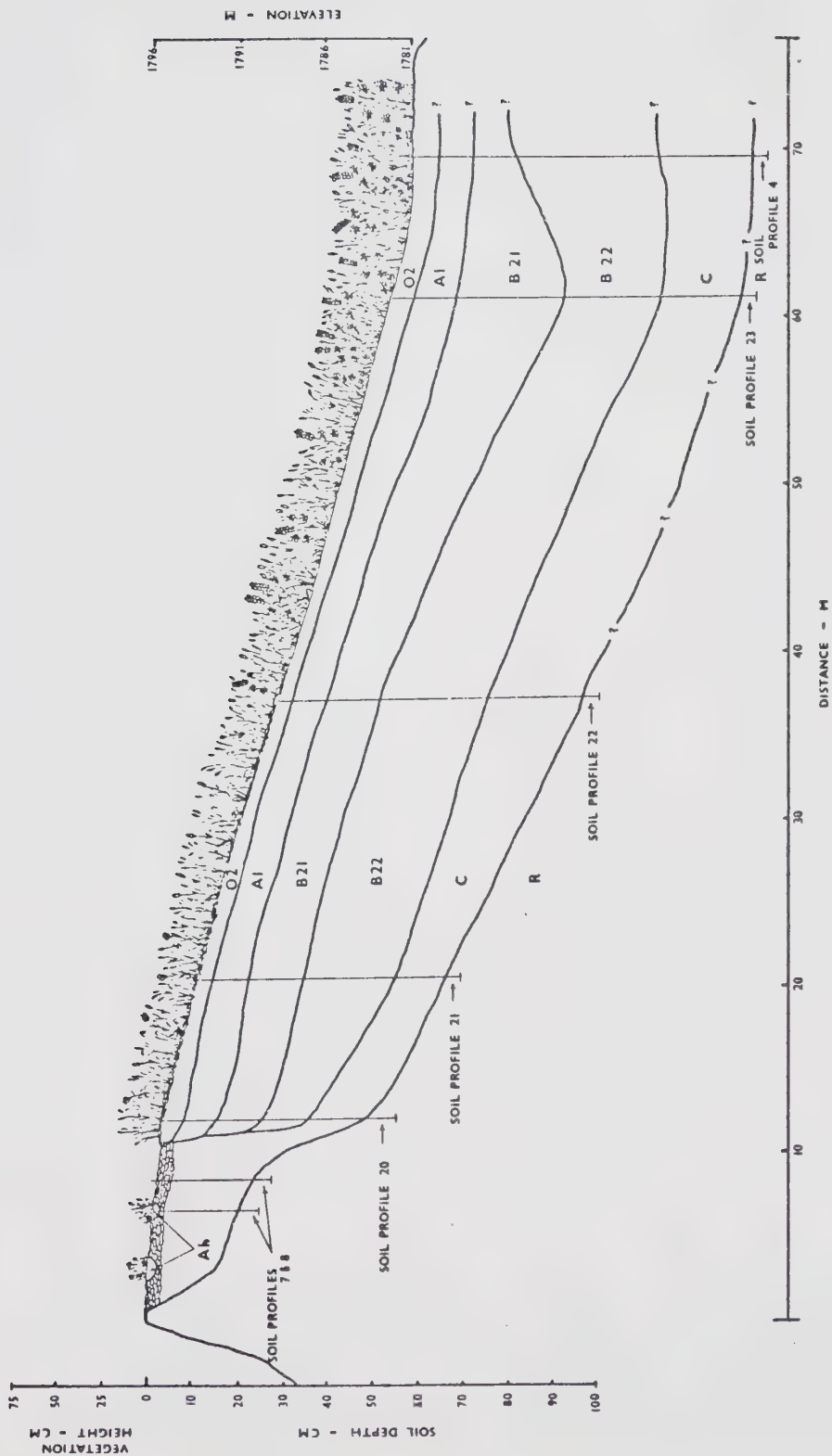


Table 6 (continued)

Species	Distance downslope (m)																																		
	1	2	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65		
<u>Achillea millefolium</u>																																			
var. <u>alpicola</u>					6		34									31	22	22		6	2	31													
<u>Vaccinium caespitosum</u>				2	38	66	90		2		2	14	108	38	86	126	14																		
<u>Agrostis scabra</u>				2	22	14	31	50	14	2	2																								
<u>Saxifraga ferruginea</u>																																			
<u>Lupinus latifolius</u>																																			
var. <u>subalpinus</u>																																			
<u>Erigeron peregrinus</u>																																			
<u>Potentilla flabellifolia</u>																																			
<u>Danthonia intermedia</u>																																			
<u>Aster foliaceus</u>																																			
<u>Agoseris aurantiaca</u>																																			
<u>Deschampsia atropurpurea</u>																																			
<u>Carex pachystachya</u>																																			
DRYOPHYTES																																			
<u>Polytrichum piliferum</u>	P	P	22	6	6	6	75	75	285	12	2	12	12	6																					
<u>Heterocladium dimorphum</u>	P	2	6	2	65	2			6	12	63	2	22	2	2																				
<u>Tortula ruralis</u>			2	2	2																														
<u>Polytrichum juniperinum</u>						2	6	12	2	6	P	63	2	22	P	63	2	2																	
<u>Pohlia</u> sp.																																			
<u>Lophozia</u> sp.																																			
<u>Distans tauricum</u>																																			
<u>Bryum</u> cf. <u>angustirete</u>																																			

Table 6 (continued)

Species	Distance downslope (m)																			
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39
LICHENS																				
<i>Cetraria ericetorum</i>	2	P	22	2	31	40	150	105	100	50	170	100	195	195	50	75	25	75	50	6
<i>Thamnolia subuliformis</i>	2	P	22	2	18	12	12	2	2	2										
<i>Cladonia mitis</i>	P	P	22	6	63	40	305	380	335	240	290	335	430	575	380	18	75	50	31	2
<i>Cladonia</i> sp.	2	2	2	2	6	6	18	2	6	18	6	6	6	2	2					
<i>Peltigera canina</i>	P	2	2	2	2	12	6		2	2										
<i>Cornicularia aculeata</i>		6	P	12	6			2												
<i>Cladonia gracilis</i>	2	2	18	40	25	75	25	25	120	86	285	170	240	125	150	195	165	63	22	
<i>Stereocaulon alpinum</i>	2	P	22	2	31	126	25	31	14	14									2	
<i>Cetraria subalpina</i>	2																			
<i>Lecidea</i> sp.				2						6	2									
<i>Lecanora</i> sp.													6							

^a P indicates that the species was present but not tallied in the plots.

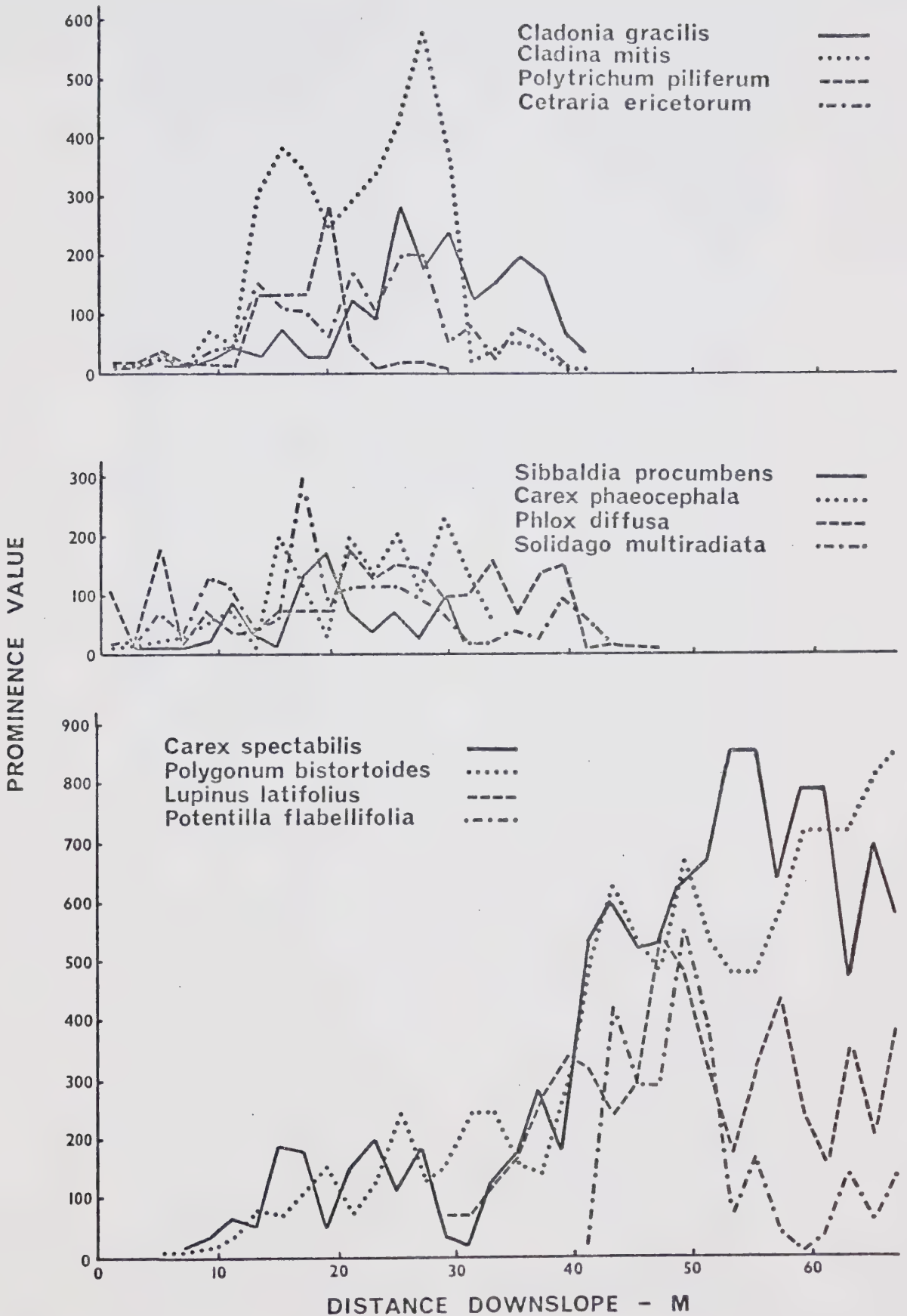
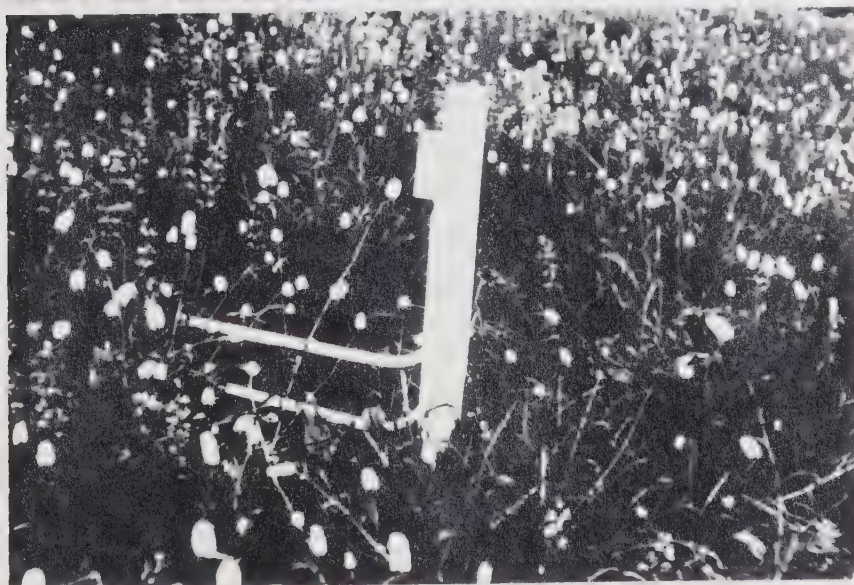
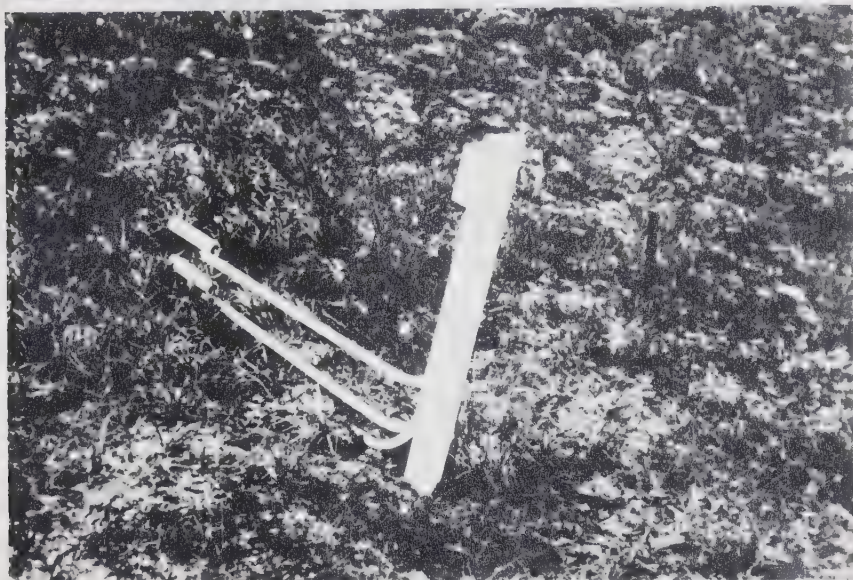
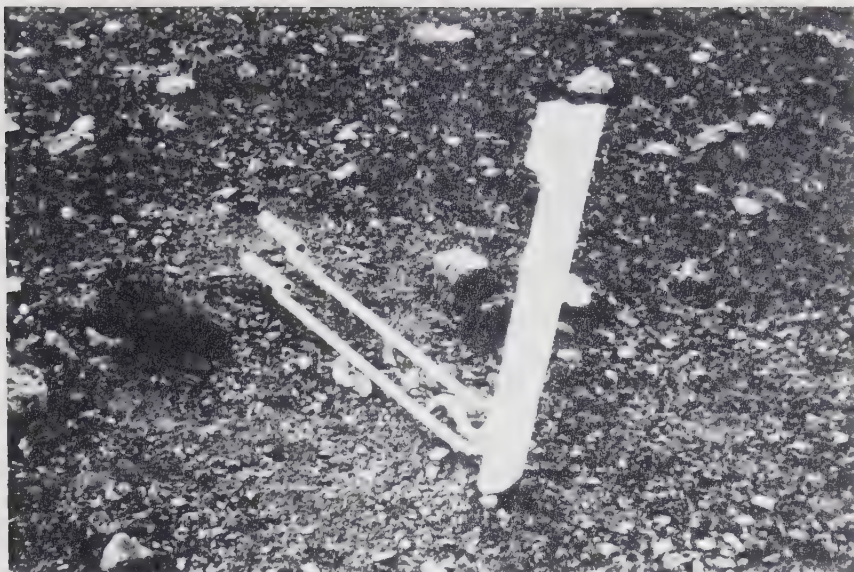


Figure 14. Distribution and abundance of major plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.

Figure 15. Vegetation along an environmental gradient at 1900 m on Grouse Ridge, Washington. The fell-field (upper) is characterized by a sparse plant cover. Farther downslope (middle) the *Carex phaeocephala*, *C. spectabilis*, and *Cladina mitis* are prominent species. At the base of the slope (lower) *Polygonum bistortoides* and *Carex spectabilis* are dominants. Air temperature sensors are located at +5 and +15 cm at the upper and middle stations and +10 and +20 cm at the lower station.



slight (less than 11%), the vegetation occurs in patches (total cover 2 to 60%) among the frost-shattered rocks. *Phlox diffusa*, *Solidago multiradiata*, *Silene parryi*, and the lichen *Cladina mitis* are the most prominent plants in this fellfield habitat (Table 6).

Farther downslope (11 to 13 m) the slope angle increases to 27% and the vegetation is essentially continuous. Total cover is higher (85 to 112%) with *Phlox diffusa*, *Solidago multiradiata*, *Carex phaeocephala*, *Carex spectabilis*, and *Polygonum bistortoides* dominating the vegetation. *Cladina mitis*, *Cetraria ericetorum*, *Cladonia gracilis*, and *Polytrichum piliferum* are important cryptogams in the understory.

Total cover continues to increase downslope reaching a maximum of 156 to 217% at the base of the slope where the slope angle is near level. From about 41 m downslope *Carex spectabilis*, *Polygonum bistortoides*, *Lupinus latifolius* var. *subalpinus*, and *Potentilla flabellifolia* become the major dominants, while other vascular plants and cryptogams are of low prominence. *Claytonia lanceolata*, although absent at the time of the vegetation survey, had a mean cover of 29% and a frequency of 100% at the base of the slope during early July.

Plant diversity

Alpha diversity measurements were applied to slope contour samples at 2 m intervals along the environmental gradient. Trends of richness (S) and general diversity (\bar{H})

are similar (Fig. 16). They are relatively low ($S = 14$, $\bar{H} = 1.29$) in the fellfield and increase to a high ($S = 29$, $\bar{H} = 2.83$) in the ecotonal area between the fellfield and the continuous vegetation. With increasing distance down-slope S and \bar{H} decline, reaching minimum $S(4)$ and \bar{H} (1.02) values near the base of the gradient.

Equitability (E) trends are not readily evident (Fig. 16). The lowest E (0.48) occurs in the fellfield where a single species (*Phlox diffusa*) dominates the site. The remainder of the gradient has E values fluctuating between 0.66 and 0.93.

Soils

The soils of the environmental gradient vary markedly from the poorly developed Entisols in the fellfield to the relatively better developed Inceptisols found on the remainder of the slope (Fig. 13). The fellfield soils show no profile development except for thin, surficial A horizons beneath the scattered clumps of vegetation. Profile 8 illustrates the characteristics of these soils under vegetation.

Horizon	Description
A1	0 to 5 cm; black (10 YR 2/1) gravelly sandy loam; structureless single grain; friable; abundant very fine to medium roots; very strongly acid (pH 4.8); clear, wavy boundary.
C	5 to 18 cm; dark brown (7.5 YR 3/2) gravelly

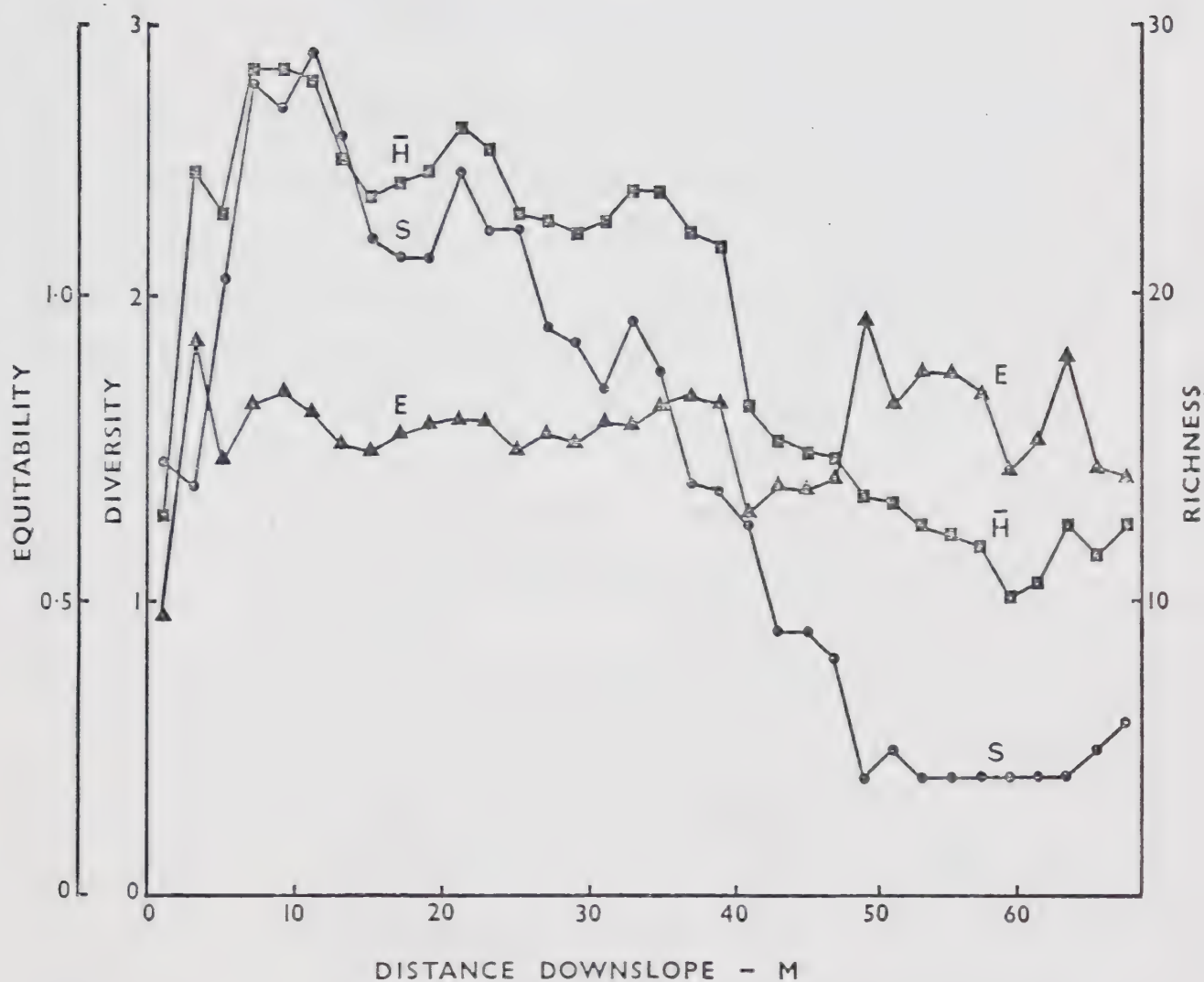


Figure 16. Relationship between species richness (S), general diversity (\bar{H}), and equitability (E) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington.

Horizon	Description
	sandy loam; structureless single grain; friable; abundant very fine to medium roots; very strongly acid (pH 4.7); abrupt, wavy boundary.
R	18 to 25 cm +; weathered shale.

The major portion of the gradient is characterized by Inceptisols beneath continuous vegetation. The horizons, except for increased thickness downslope, show only slight morphological variation. The profile (20) below is typical of soils near the top of the slope.

Horizon	Description
01	3 to 2 cm; fresh herbaceous litter.
02	2 to 0 cm; partially humified herbaceous litter.
A1	0 to 7 cm; dark reddish brown (5 YR 2/2) sandy loam; structureless, single grain; very friable; abundant very fine roots; very strongly acid (pH 4.5); gradual, smooth boundary.
B21	7 to 17 cm; very dark grayish brown (10 YR 3/2) sandy loam; weak, very fine crumb structure; friable; abundant very fine to fine roots; very strongly acid (pH 4.9); gradual, smooth boundary.
B22	17 to 28 cm; very dark grayish brown (10 YR

Horizon .	Description
	3/2) sandy loam; weak, fine crumb structure; friable; plentiful very fine roots; very strongly acid (pH 5.0); abrupt, wavy boundary.
C	28 to 40 cm; dark yellowish brown (10 YR 3/4) sandy loam; weak, fine crumb structure; friable; very few very fine roots; strongly acid (pH 5.2); abrupt, smooth boundary.
R	40 to 45 cm +; weathered shale.

Soils reach their greatest depths at the base of the slope. The following profile (4) characterizes the lower slope soils:

Horizon	Description
01	5 to 4 cm; fresh herbaceous litter.
02	4 to 0 cm; partially humidified herbaceous litter.
A1	0 to 8 cm; black (10 YR 2/1) sandy loam; structureless, very friable; abundant, very fine to medium roots; extremely acid (pH 3.9); gradual, wavy boundary.
B21	8 to 18 cm; dark reddish brown (5 YR 2/2) sandy loam; weak crumb structure; friable; abundant, very fine to fine roots; extremely acid (pH 4.0); gradual, wavy boundary.
B22	18 to 50 cm; dark reddish brown (5 YR 2/2)

Horizon	Description
	sandy loam; weak, very fine crumb structure; friable; plentiful very fine to fine roots; very strongly acid (pH 4.5); gradual, smooth boundary.
C	50 to 70 cm +; dark yellowish brown (10 YR 3/4) gravelly sandy loam; very fine crumb structure; friable; few very fine to fine roots; very strongly acid (pH 4.8).

Physical and chemical properties were determined for seven profiles along the environmental gradient (Table 7). All properties were comparable to those found in similar communities in the western North Cascades. Organic matter, total exchange capacity, exchangeable cations, available phosphorus and potassium were highest, while pH was lowest, at the base of the slope (Table 7). Sand/silt to clay ratios are relatively high throughout the gradient.

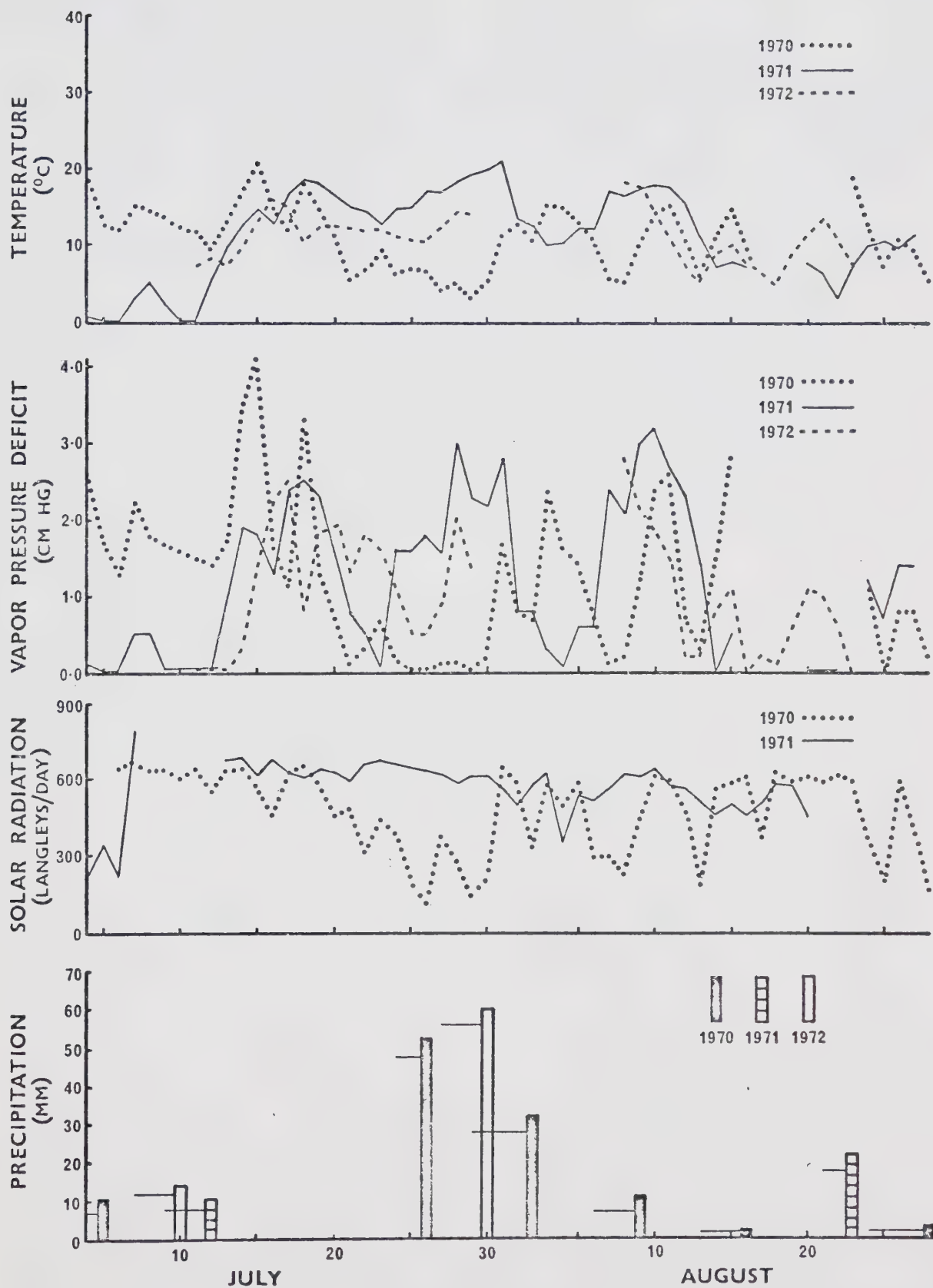
Mesoclimate

The general environmental data for Grouse Ridge were presented in a previous section (Table 5). A more detailed account of the mesoclimate appears in Fig. 17. Patterns of temperature, VPD, solar radiation, and precipitation fluctuate markedly, both during and between summers, in this maritime type alpine region.

TABLE 7. Physical and chemical properties from seven soil profiles along an alpine environmental gradient, Grouse Ridge, Mt. Baker, Washington.

Downslope distance (m)	Profile	Horizon	pH	Texture			Organic matter (%)	Available			Exchangeable cations (me/100 g)				TEC (me/100 g)
				Sand (%)	Silt (%)	Clay (%)		N (ppm)	P (ppm)	K (ppm)	Na	K	Ca	Mg	
4	7	C1	4.7	47.0	40.1	13.9	2.9	-	-	-	0.05	0.12	0.25	0.20	14.3
		C2	4.6	53.8	39.6	6.6	-	-	-	-	-	-	-	-	-
6	8	A1	4.8	49.2	47.0	3.8	1.4	2.5	40.0	115.0	0.04	0.19	1.25	0.70	14.5
		C1	4.7	65.1	27.8	7.1	0.8	2.5	13.0	75.0	0.00	0.14	0.73	0.37	17.5
12	20	A1	4.5	60.2	22.8	17.0	18.1	1.0	1.5	115.0	0.05	0.28	0.75	0.49	30.6
		B21	4.9	61.1	20.5	18.4	11.9	0.0	1.0	52.5	0.11	0.11	0.28	0.20	27.4
		B22	5.0	58.7	24.0	17.3	7.9	0.0	1.0	30.0	0.02	0.05	0.25	0.08	25.1
		C	5.2	64.1	25.9	10.3	-	-	-	-	-	-	-	-	-
21	21	A1	4.3	61.0	22.6	16.4	20.4	0.5	3.0	87.5	0.00	0.24	0.70	0.45	38.8
		B21	4.8	60.8	20.1	18.1	10.4	0.0	3.0	27.5	0.11	0.05	0.20	0.08	27.6
		B22	4.9	59.7	22.1	18.2	7.1	0.0	4.5	12.5	0.02	0.03	0.25	0.04	19.8
		C	5.1	66.1	22.4	11.5	-	-	-	-	-	-	-	-	-
38	22	A1	4.3	60.3	22.5	17.2	20.4	1.0	17.5	110.0	0.00	0.33	1.00	0.70	36.7
		B21	4.9	62.3	19.8	17.9	10.6	0.0	2.5	40.0	0.02	0.07	0.25	0.04	26.2
		B22	5.0	61.7	20.5	17.8	6.7	0.0	6.0	15.0	0.00	0.03	0.00	0.00	18.7
		C	5.1	71.2	18.4	10.4	-	-	-	-	-	-	-	-	-
62	23	A1	4.4	60.5	21.7	17.8	17.9	3.5	45.5	177.5	0.00	0.51	1.88	0.94	30.1
		B21	4.6	61.7	19.8	18.5	10.0	1.5	14.5	75.5	0.02	0.17	0.25	0.16	22.3
		B22	4.9	60.2	21.9	17.9	7.6	0.5	7.5	35.5	0.01	0.06	0.20	0.08	23.1
		C	5.1	65.1	24.8	10.1	-	-	-	-	-	-	-	-	-
69	4	A1	3.9	61.2	21.7	17.1	21.6	1.0	60.0	201.5	0.10	1.14	8.00	2.95	40.5
		B21	4.0	61.3	20.5	18.2	9.8	3.5	49.0	132.5	0.02	0.33	0.45	0.08	21.7
		B22	4.5	59.8	24.3	16.9	7.0	5.0	35.0	72.5	0.03	0.17	0.28	0.08	19.3
		C	4.8	67.0	22.3	10.7	-	-	-	-	-	-	-	-	-

Figure 17. Seasonal variation in temperature, VPD, solar radiation, and precipitation at the Grouse Ridge weather station during 1970, 1971, and 1972. Vertical lines adjacent to the precipitation bars represent the period over which the precipitation reading was accumulated.



Microclimate

To obtain information on the microclimate of the environmental gradient air temperatures (+5 and +15 cm at 4, 19, and 36 m downslope and +10 and +20 cm at 61 m downslope), soil profile temperatures (-2 and -10 cm on both vegetated and non-vegetated sites at 4 m downslope and -10, -20, and -30 cm at 19, 36, and 61 m downslope), and soil moisture regimes (-5 cm on both vegetated and non-vegetated sites at 4 m downslope, -10 and -20 cm at 19 and 36 m downslope, and -10 and -30 cm at 61 m downslope) were monitored along the transect. These stations were located at 4, 19, 36, and 61 m downslope.

Seasonal temperature profiles along the transect vary considerably from the top of the ridge to the base of the slope although all stations have the same increasing seasonal pattern (Figs. 18 and 19). Fellfield air (+5 and +15 cm) temperatures at the top of the transect, in contrast to those on the remainder of the slope, were usually lower than temperatures at subsurface depths. Highs of near 35°C were reached several times during 1971 and 1972 at -2 cm. These high subsurface temperatures are due mainly to a higher surface albedo and the low heat capacity of the moisture-poor substratum. Maximum near-surface temperatures of 49°C have been reported in other high elevation studies in western North America (Bamberg and Major, 1968; Ballard, 1972). Temperatures beneath vegetation were generally 2 to 3° higher than for adjacent non-vegetated sites. Average

Figure 18. Seasonal variations in soil and air temperature profiles at various heights (cm) and depths (cm) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971. The dotted line represents the daily maximum air temperature at an adjacent weather station. Temperature profile data are for readings taken between 1300 and 1500 hr. Soil temperatures in the fellfield (4 m downslope) were monitored on both non-vegetated (NV) and vegetated (V) sites.

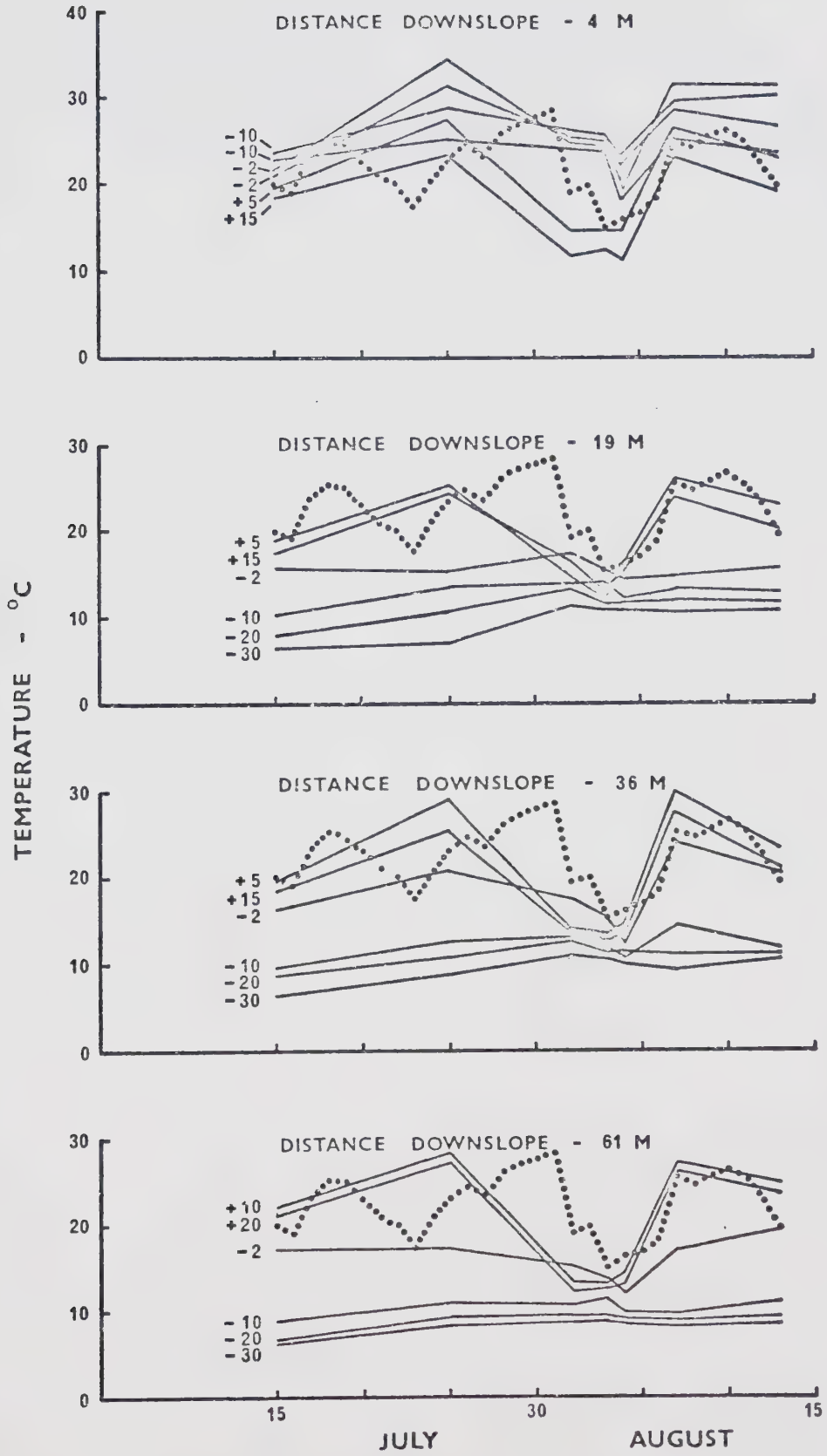
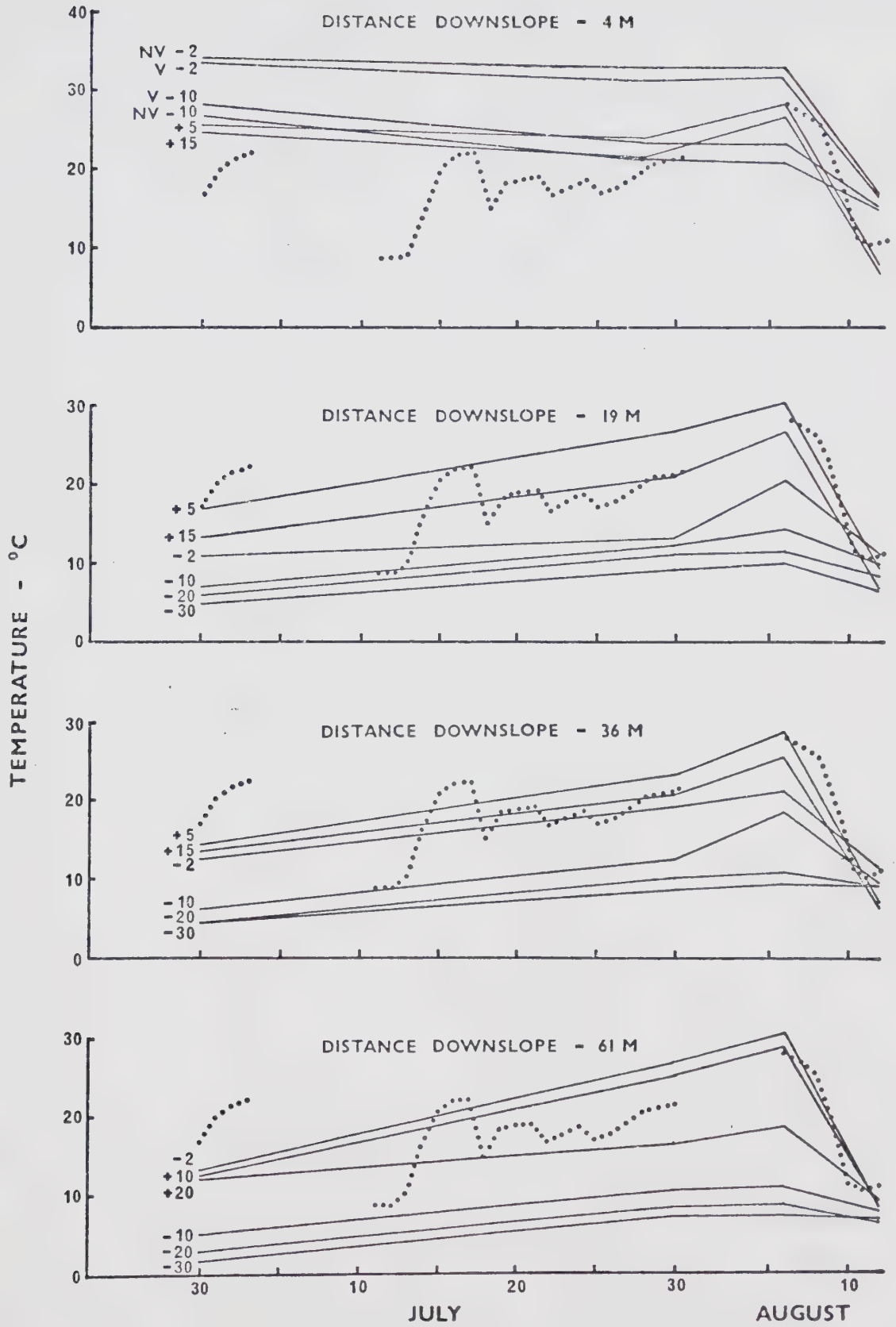


Figure 19. Seasonal variations in soil and air temperature profiles at various heights (cm) and depths (cm) along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1972. The dotted line represents the daily maximum air temperature at an adjacent weather station. Temperature profile data are for readings taken between 1300 and 1500 hr. Soil temperatures in the fellfield (4 m downslope) were monitored on both non-vegetated (NV) and vegetated (V) sites.



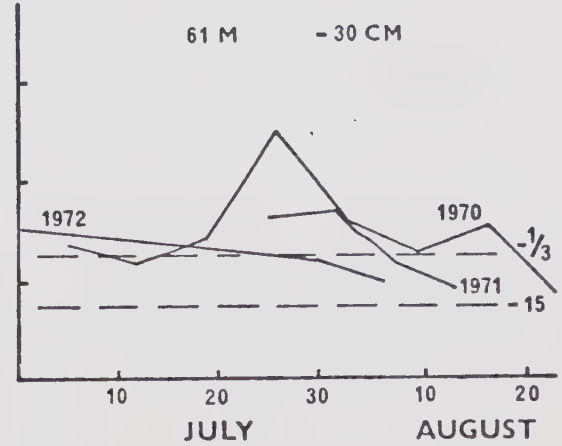
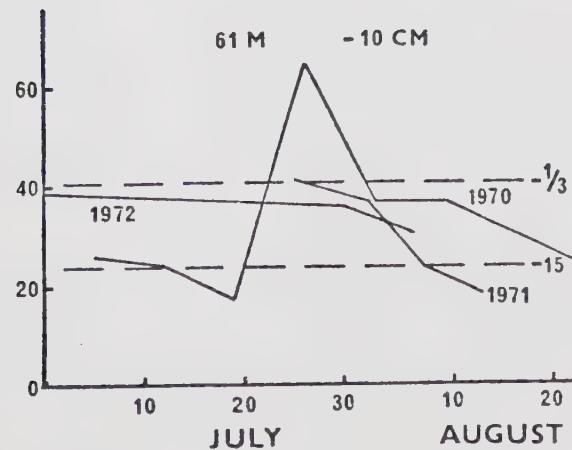
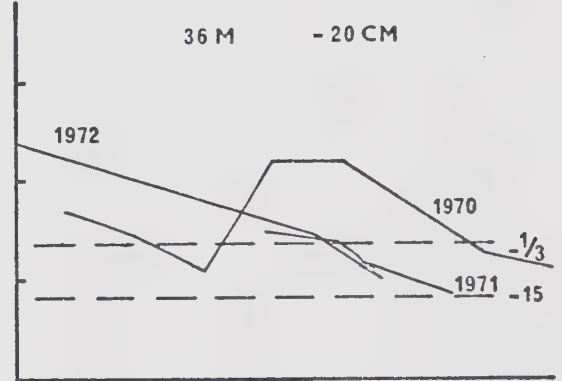
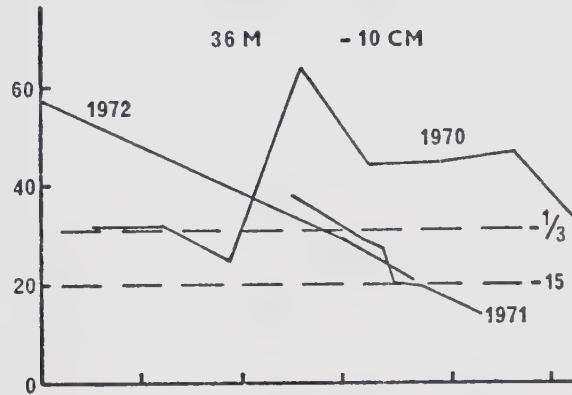
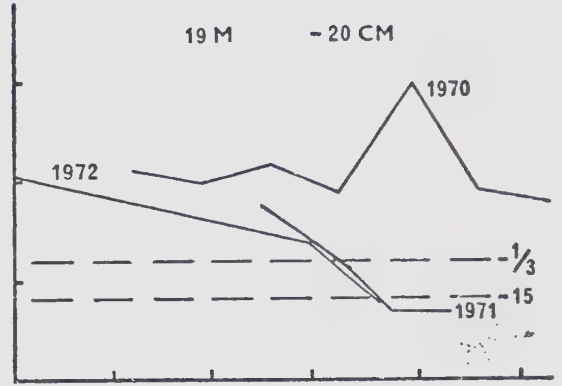
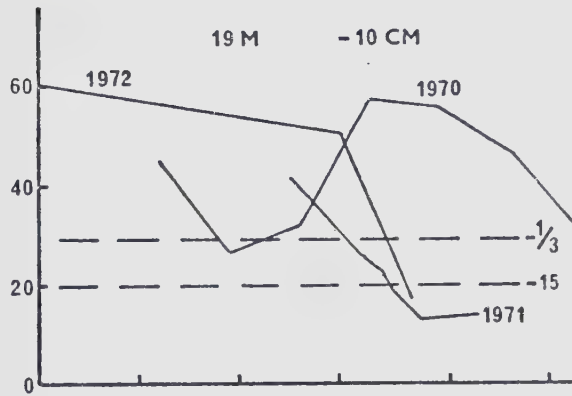
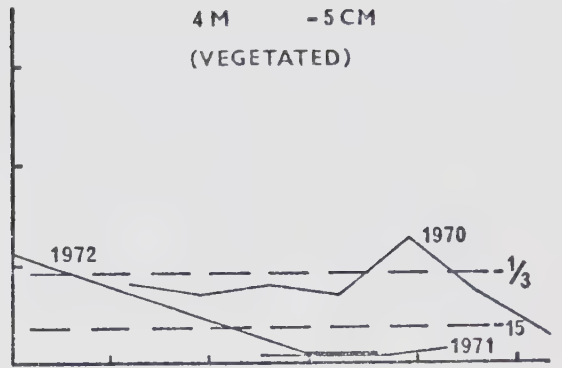
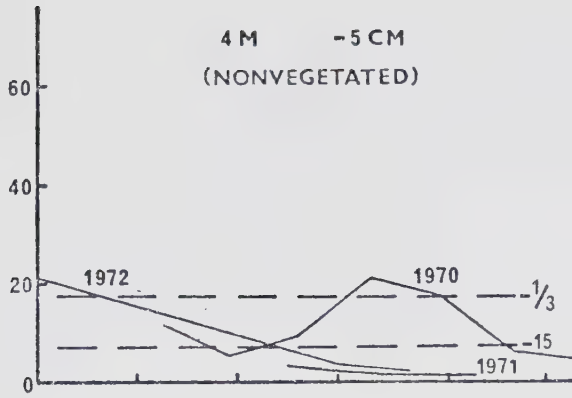
temperatures at -10 cm in the fellfield are about 7 to 8°C less than that at -2 cm.

Subsurface temperatures along the remainder of the transect show sharp vertical gradients over relatively short distances. The steepest gradients are between the surface and -10 cm level. These profile temperature gradients remain relatively constant throughout the summer except during periods of rapidly decreasing air temperatures. Temperatures at -10 to -30 cm decrease slightly (2 to 4°C) with distance downslope. This reflects the insulation afforded by the greater degree of vegetative cover.

Soil moisture along the environmental gradient closely parallels the summer precipitation pattern. This was especially evident in 1970 (Fig. 20) when frequency of summer rainfall was high (Fig. 17) and soil moisture regimes fluctuated accordingly. Soil moisture declined steadily throughout the summers of 1971 and 1972 due to low precipitation. The increase in soil moisture immediately after the 6.6 cm of precipitation during the latter part of July 1972 (Fig. 17) is not reflected in Fig. 20 due to reading dates. The use of the -15 bar soil water potential to estimate the permanent wilting percentage is somewhat questionable (Slatyer, 1967), especially since it is based on information from crop plants. This field soil parameter is still useful, however, when used with caution. Soil moisture usually remains well above -15 bars until mid-August, except in the fellfield where levels often fall

Figure 20. Soil moisture regimes along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1970, 1971, and 1972. Distance (m) downslope and depth (cm) appear on each graph. The $-1/3$ and -15 bar tensions for the soil are indicated by the horizontal dashed lines.

SOIL MOISTURE - % OVEN DRY WEIGHT



below -15 bars by mid-July. Soil moisture stress increases slightly, with distance, down the continuously vegetated portion of the transect during drought periods. This is likely due to the greater transpiration losses associated with increased plant cover (or increased total leaf area) downslope.

Physiology

Leaf water potentials (ψ) of eight plant species along the environmental gradient, and two other nearby species, were measured during and after a drought period in 1971 (Table 8). The readings for each species at each site were relatively consistent with standard deviations varying between 0.3 and 1.5 bars. The first measurements were taken on July 20 after a one-week period without precipitation. The lowest leaf ψ (-13.8 to -15.0 bars) were obtained 20 m downslope, an area that had been snow-free for 4 to 5 weeks. Readings in the fellfield and at 40 to 43 m downslope were also relatively low (-11.8 to 13.8 bars). Higher leaf ψ of -5.0 to -5.1 were recorded at the base of the slope, an area that had been snow-free for only three weeks.

Measurements taken 24 days later showed only slightly lower leaf ψ although soil ψ had markedly decreased (Fig. 20). The lowest leaf ψ for most species was recorded at this time. *Lupinus latifolius* (at 21 m downslope) and *Phyllodoce empetriformis* (adjacent to the transect at about 25 m downslope) reached lows of -27.4 and -22.1 bars, respectively. The *Lupinus* plants were wilted at this time

TABLE 8. Seasonal leaf water potential (bars) of 10 plant species along an environmental gradient on Grouse Ridge, Mt. Baker, Washington during 1971. Data are means of at least three readings taken between 1300 and 1500 hr; except those in parentheses which were taken at 2400 hr.

Species	Downslope distance (m)	Date		
		July 20	August 13	August 30
<i>Lupinus lepidus</i>	1		-13.8	
<i>Solidago multiradiata</i>	5		-15.2	
<i>Solidago multiradiata</i>	7	-11.9	-13.1	
<i>Polygonum bistortoides</i>	7		-17.9	
<i>Polygonum bistortoides</i>	9	-13.8	-15.5	
<i>Solidago multiradiata</i>	19	-15.0	-15.9	-15.1
<i>Polygonum bistortoides</i>	19	-15.0	-17.9	-15.2 (-4.5)
<i>Lupinus latifolius</i>	19		-27.4	
<i>Vaccinium caespitosum</i>	21	-13.8	-14.1	-17.0 (-7.9)
<i>Erigeron peregrinus</i>	21		-17.2	
<i>Polygonum bistortoides</i>	36	-11.8	-12.4	
<i>Lupinus latifolius</i>	36	-12.0	-12.9	
<i>Aster foliaceus</i>	43			-11.0 (-5.5)
<i>Polygonum bistortoides</i>	61	-5.1	-5.2	-5.8 (-2.1)
<i>Lupinus Latifolius</i>	61	-5.0	-5.5	
<i>Lupinus latifolius</i>	63		-7.6	-9.2 (-3.4)
<i>Castilleja miniata</i>	Not on transect		-16.2	
<i>Vaccinium deliciosum</i>	Not on transect	-10.2	-12.4	-8.3 (-6.5)
<i>Phyllodoce empetriformis</i>	Not on transect	-15.6	-22.1	-21.9

and died back several days later. The *Phyllodoce empetri-formis* plants appeared normal. Other species reached lows of -12.4 to -17.9 bars. At this time soil ψ was about -14 bars at 19 m downslope and -14 to -17 bars at 36 m downslope. Similar lows have been reported from the Olympic Mountains by Kuramoto and Bliss (1970) and Peterson (1971).

A third set of readings was obtained on August 30, seven days after a light rain (2.2 cm). Most plants were dispersing seeds at this time. Leaf ψ , except for *Vaccinium caespitosum*, were slightly higher for species near the top of the slope. The lowest leaf ψ for species at the base of the slope were reached at this time. These leaf ψ were still much higher than those attained by the same species upslope. Readings showed high diurnal amplitudes with species increasing by as much as 10.7 bars at 2400 hr from their afternoon lows. Therefore, the plants could, in fact, spend part of the day at a lower leaf ψ and still be photosynthetically active in the morning. Kuramoto and Bliss (1970), working in the Olympic Mountains, Washington, found that at a soil ψ of -15 bars, *Festuca*, *Lupinus*, and *Eriophyllum* sp. still maintain a photosynthetic rate approximately 40% that at -0.3 bars.

Phenology

Plant phenology can often be helpful in describing microenvironmental differences between various habitats (Bliss, 1962) as well as long environmental gradients. During the summers of 1971 and 1972, 32 species were

observed at 10 m intervals along the transect.

Phenological phases varied considerably among species along the gradient (Fig. 21). Length of a given phenological phase was relatively consistent within species, regardless of the year or position on the slope.

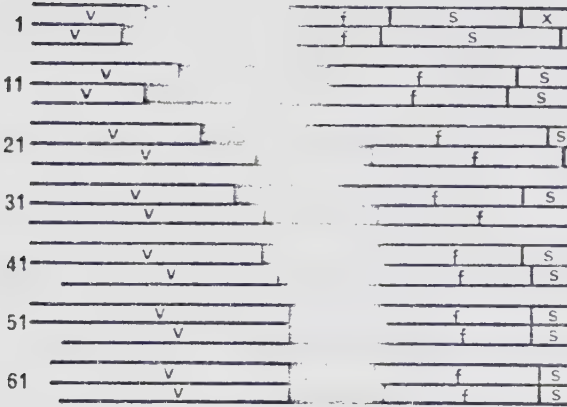
Snow release took place at about the same time in both 1971 and 1972. The upper part of the slope was free of snow by June 18 and at the base by June 28. The much higher temperatures in late June and early July during 1972, however, resulted in more vigorous vegetative growth and an earlier flowering for most species. This was especially notable in the upper part of the gradient. *Silene parryi*, in the fellfield, and *Potentilla flabellifolia*, at the base of the transect, were exceptions to this pattern.

At any given point on the environmental gradient most of the species have similar flowering phases, an indication that local microenvironments govern phenological development (Bliss, 1956). The most notable exceptions to this were the late development of *Aster foliaceus* and the early development of *Claytonia lanceolata*. In general most species flowered 14 to 24 days after initiation of growth. They remained in flower for 8 to 20 days before entering a 10 to 24 day fruiting stage prior to seed dispersal.

Figure 21. Phenological patterns of 12 plant species on Grouse Ridge, Mt. Baker, Washington during 1971 (upper bar) and 1972 (lower bar). Distance (m) downslope appears on the ordinate axis; month and day are on the abscissa.

Symbols are: v - vegetative growth, solid bar - in flower, f - in fruit, s - seed dispersal, x - signs of dormancy.

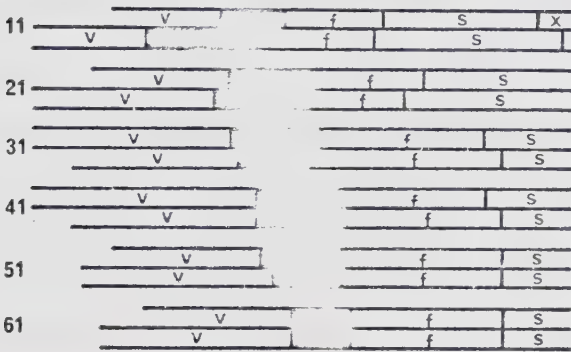
Polygonum bistortoides



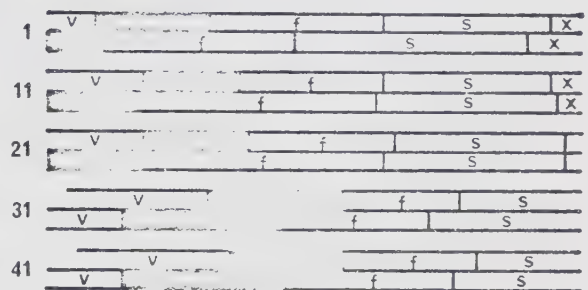
Carex spectabilis



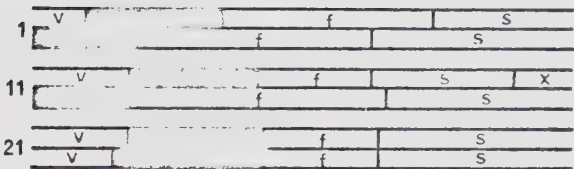
Lupinus latifolius



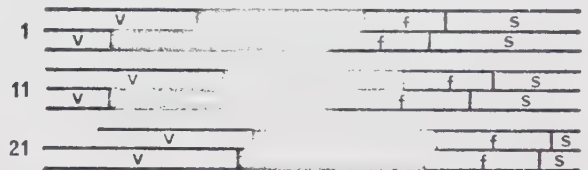
Phlox diffusa



Carex phaeocephala



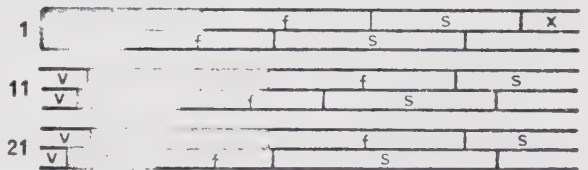
Solidago multiradiata



Silene parryi



Sibbaldia procumbens



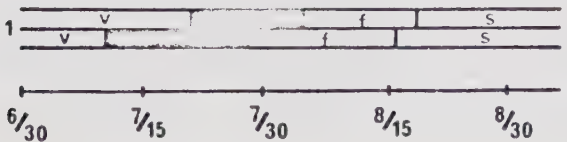
Festuca ovina



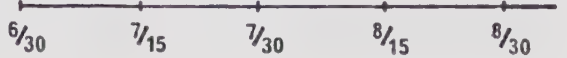
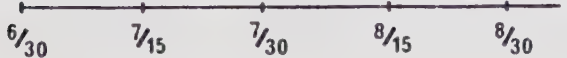
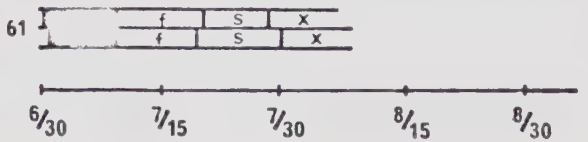
Potentilla flabellifolia



Saxifraga bronchialis



Claytonia lanceolata



DISCUSSION

Community Pattern

Distribution of alpine plant communities in the North Cascades is a response to complex environmental factors and environmental gradients. When environmental gradients are steep, abrupt changes in species composition occur, creating a mosaic of plant communities on the landscape. If these gradients are gentle then more gradual changes create a continuum. In the North Cascades the mosaic pattern is more common, especially in the western and central portions of the range. This is due to the more complex topography and greater snowfall which results in variable snow release times and a broad range of summer soil moisture regimes. These environmental factors are also of prime importance in the eastern North Cascades, but to a lesser extent. In the eastern North Cascades the more gentle topography, lower snowfall, and shorter range of snow release times result in a more gradual shift in community pattern.

The importance of snowmelt time is demonstrated by the two-dimensional ordinations (Fig. 3) of the major community types. These ordinations illustrate the relationships between the community types and their correlation with snowmelt time. The date of snowmelt also determines the summer soil moisture regime, at least for the earlier, and probably the most important part of the growing season.

In the western North Cascades a distinct mosaic appears

repeatedly on the landscape. Snow depth and snowmelt time varies considerably. In snowbank sites communities are dominated by *Carex nigricans* unless the soils are unstable, in which case the *Saxifraga tolmiei*-*Luzula wahlenbergii* community occurs.

On better drained habitats where snowmelt is earlier, the heath communities, dominated by either *Cassiope mertensiana*, *Phyllodoce empetrifolia*, *P. glanduliflora*, *Arctostaphylos uva-ursi*, or *Empetrum nigrum*, are common. The latter is most frequently found on exposed or northerly aspects. Exposed sites with slightly earlier snowmelt times are dominated by *Salix cascadiensis* or *S. reticulata*.

Communities on warm, moist southerly slopes are dominated by the *Lupinus latifolius* type. The closely related *Carex spectabilis* community occurs on similar, but slightly drier slopes. Where the earliest snowmelt occurs the sites become relatively dry by mid-summer and are dominated by *Carex phaeocephala*.

On ridgetops, which remain snow-free most of the winter, blockfields are typical. These sites may be occupied by a variety of species, either in clumps, where the surface is stable, or in vegetation stripes where slow downslope creep takes place. Prominent plants in these habitats are *Phlox diffusa*, *Potentilla diversifolia* var. *diversifolia*, *Solidago multiradiata*, *Oxytropis campestris* var. *gracilis*, and *Carex albonigra*.

Changes in macroclimate in an easterly direction

result in gradual changes in the vegetation pattern. Lower snow accumulation, slightly earlier snowmelt, and somewhat drier and warmer summers in the central North Cascades result in the absence of some communities and the appearance of others. Late melting snowbanks are still occupied by *Carex nigricans* but snow accumulation sites that become snow-free earlier are dominated by *Antennaria lanata* or *Carex breweri*. *Antennaria lanata* communities often occur in close proximity to the *Carex nigricans* type, but the former are better drained and become drier in late summer. This segregation of communities within an alpine snowbank site was also noted in the Presidential Range of New Hampshire (Bliss, 1963), the Rocky Mountains (Billings and Bliss, 1959; Johnson and Billings, 1962) and the Olympic Mountains of Washington (Bliss, 1969). In unstable snow accumulation areas in the central North Cascades the *Eriogonum pyrolae-folium*-*Luzula wahlenbergii* community replaces the *Saxifraga tolmiei*-*Luzula wahlenbergii* community.

The same heath communities found to the west again occupy similar habitats in the central region. Communities dominated by *Salix cascadiensis* or *S. reticulata* also occupy drier exposed slopes. The driest of these exposed slopes, and some of the ridgetops, are characterized by extensive mats of *Dryas octopetala*.

Warm, moist southerly slopes are again occupied by *Lupinus latifolius* but the closely related *Carex spectabilis* community is apparently replaced on drier central region

sites by *Festuca viridula*. *Carex phaeocephala* again dominates sites that are snowfree earlier, but on the most exposed upper slopes *Carex nardina* becomes the most prominent species.

The blockfields in this region are also extremely variable in plant and rock cover, and species composition. Important plants are *Selaginella densa*, *Phlox diffusa*, *Carex phaeocephala*, and *Arenaria capillaris*, and farther south, *Phlox hendersonii* and *Lupinus lepidus* var. *lobbii*.

The dry, warm summers and lower winter snowfall in the eastern North Cascades provide community patterns that are in marked contrast to those in the western North Cascades. Although mosaic patterns are still common, many extensive slopes show gradual changes in species composition in response to more gentle environmental gradients.

Numerous snowbank communities occur in this region. *Carex nigricans* is essentially restricted to the subalpine zone with *Antennaria lanata* or *Carex breweri* dominating the alpine sites where snow accumulation is greatest. Snowbed sites that open slightly earlier are occupied by *Phyllodoce empetrifolia*, *P. glanduliflora*, or *Salix cascadiensis*. At higher elevations level areas or depressions, which receive moisture for much of the summer from upslope, are dominated by *Carex capitata*.

On well drained habitats where snowmelt is earlier, communities may be dominated by *Carex phaeocephala*, *Arctostaphylos uva-ursi*, *Salix cascadiensis*, *S. reticulata*, or

Dryas octopetala, with the latter two occupying the driest sites. At lower elevations in the alpine and subalpine zones of the eastern region, where soil moisture levels are greater, broad expanses are dominated by *Danthonia intermedia*. Upslope, this community often grades into the *Carex scirpoidea* var. *pseudoscirpoidea* type, another extensive community.

The driest of the major alpine communities occur on the higher slopes and summits. These are dominated by *Carex nardina*, *Calamagrostis purpurascens*, or *Kobresia myosuroides*. The topographical position of the *Kobresia myosuroides* community suggests that these sites are essentially free of snow with ephemeral microdrifts occurring during the winter, such as Bell (1973) reports for this type in the Rocky Mountains of Colorado. The *Calamagrostis purpurascens* stands often occur in rocky sites within larger *Kobresia* communities. These rocky sites may provide slightly better protection during the winter.

The blockfields, which occupy the driest, snowfree ridgetops, vary considerably in composition. *Lupinus lepidus* var. *lobbii*, *Arenaria obtusiloba*, and *Festuca ovina* var. *brevifolia* are prominent species.

The overstory composition of krummholz stands changes markedly across the North Cascades. In the western part of the range *Abies lasiocarpa* predominates. The latter species, along with *Picea engelmannii* and *Larix lyallii*, is common in the central North Cascades. Farther east *Picea engelmannii*

and *Pinus albicaulis* dominate the krummholz stands.

Regional separation on the basis of understory composition is inconsistent due to considerable variation in composition and the distribution of several important species across the entire range (Table 3).

Community-soil relationships

Jenny (1941) related that any soil property is a function of the regional climate, parent materials, topography, biota, and time. The vegetation of a region is also a function of these factors (Major, 1951). In the North Cascades all of these factors, with the exception of the parent materials, vary considerably. This relatively uniform parent material is due, in large part, to the extensive pyroclastic deposits present in the region. These deposits, mixed with the residuum of the various geologic strata, modify the residuum to such an extent that they have no detectable influence on the regional alpine vegetation and soil patterns. This is in contrast to many regions where ultramafic (Kruckeberg, 1954, 1969; Whittaker, 1954), sandstone-dolomite (Mooney *et al.*, 1962), or calcareous (Bamberg and Major, 1968) parent materials have marked effects on vegetation and soil patterns.

The pattern of alpine soil types in the North Cascades generally corresponds to the vegetation pattern. Beneath krummholz and heath vegetation cheluviation is a common process. This process is most intense in the western North Cascades where leached A2 horizons and iron-rich B horizons

are typical. Spodosols have been studied in detail in the North Cascades (van Ryswyk, 1969; Bockheim, 1972) and have been reported from a number of other alpine areas (Bliss and Woodwell, 1965; Kuramoto and Bliss, 1970; and others).

Inceptisols are typical of many of the community types in the North Cascades, especially in the eastern part of the range. The most notable differences within the Inceptisols are the chemical characteristics, which vary markedly from west to east. The western soils usually have higher organic matter, cation exchange capacity, and nutrient levels, and are more acidic.

Sites that are unstable and sparsely vegetated are characterized by Entisols. These soils usually have only shallow A-C profiles beneath vegetation and have low organic matter, cation exchange capacity, and nutrient levels.

Alpine plant diversity patterns

The response of various components of species diversity is dependent on biotal, historical, and physical factors. In the alpine zone of the North Cascades these components (S , \bar{H} , and E) show corresponding responses at both a regional and local (environmental gradient) level (Figs. 12 and 16). Community types or vegetative units with a "mild" environment have low S , \bar{H} , and E values. These indices increase with environmental "harshness" to a point where physical factors inhibit plant establishment; and S and \bar{H} again decline.

These data support the hypothesis of del Moral (1972)

regarding species diversity regulation within terrestrial plant communities. This hypothesis states that diversity reaches a maximum at that degree of environmental rigor which prevents a closed canopy but still permits considerable specialization. Thus in the "mildest" or "harshest" habitats, which are rendered homogeneous by their physical or biotic factors, fewer species can be sustained.

In the alpine zone of the North Cascades the mildest habitats, with late snowmelt, adequate summer soil moisture, high leaf ψ , and low degree of exposure, are homogeneous and dominated by a few species (average of 14 to 26 species per stand) exhibiting high crown cover. A significant control over the composition and structure of the community is exerted either by the plants themselves (through competition) or by the exclusion of potential competitors due to the short growing season. As the alpine environment becomes more rigorous (*i.e.*, higher moisture stress and lower leaf ψ), dominance by any single species declines and allows considerable habitat heterogeneity. This allows a multitude of plants (average of 28 to 44 species per stand) to take advantage of the resulting microhabitats. Habitat homogeneity (average of 8 to 15 species per stand) is once again reached as physical harshness renders the habitat relatively inhospitable.

Recent studies indicate similar diversity responses to canopy structures (Goff and Zedler, 1968; Auclair and Goff, 1971; Douglas and Ballard, 1971; del Moral, 1972, 1973).

That is, after an initial increase, diversity declines with canopy closure or community stability.

Response of species to an environmental gradient

The environmental gradient on Grouse Ridge provided an opportunity to examine the response of various species to gradual changes in microenvironment along an alpine slope. Plant community data collected along the transect also indicate a gradual, but notable, change in structure and composition. The fellfield is characterized by sparse clumps of vegetation (total average cover of 21%), few species (average of 20 species) and low general diversity (average \bar{H} of 2.31). Near its edge, in the ecotonal area between discontinuous and continuous vegetation, species richness and general diversity reach a maximum ($S = 29$, $\bar{H} = 2.8$). Total plant cover increases to 217% while species richness and general diversity decrease ($S = 4$, $\bar{H} = 1.02$) downslope.

Soil temperature and soil moisture measurements monitored for two years indicated that high soil temperature and low soil moisture regimes are typical of the ridgetop fellfield while lower temperatures and higher moisture levels occur downslope. Soil temperature decreases slightly, while soil moisture stress increases, with distance down the vegetated portion of the slope during drought periods. The pattern of these environmental parameters is likely due to the increased vegetative cover and greater evapotranspiration rates at the base of the slope.

Measurements of leaf ψ also indicate varying responses to slope environmental gradients. Leaf ψ generally increases with distance downslope. Measurements obtained on the upper slope (at 21 m) were generally between about -14 and -18 bars, except in the case of *Lupinus latifolius* with a low of -27.4 bars. The plants, from which the latter values were obtained, died back within several days indicating that *L. latifolius* probably cannot tolerate leaf ψ much lower than that attained in *Polygonum bistortoides* (-15 to -18 bars). The highest leaf ψ (-5.2 to -9.2 bars) were measured at the base of the slope. These higher values indicate that the bulk of the water requirements of the plants are being sufficiently met from near the -30 cm level where soil moisture stress is seldom, if ever, critical (Fig. 20).

The leaf ψ values may explain the distribution pattern and relative abundance of *Lupinus latifolius*, *Polygonum bistortoides*, and *Carex spectabilis* along the gradient. At the base of the slope, where leaf ψ was never critically low (Table 8), *Lupinus latifolius*, *Polygonum bistortoides*, and *Carex spectabilis* reach their lushest and most vigorous growth, excluding almost all other plants. Farther upslope, where leaf ψ become lower, these three plants are still able to grow, but with reduced vigor. Habitat heterogeneity thus increases resulting in increasing species richness and general diversity.

The plants occurring in the fellfield are adapted to an entirely different set of environmental factors than

those downslope. *Polygonum bistortoides* and *Carex spectabilis* occur only near the edge of the fellfield in large (1 to 2 m²) clumps. These clumps are probably not snow-free during the winter, thus these plants do not have to endure the high winds, low temperatures, and frequent frost cycles common to the rest of the fellfield. The fellfield species (*Lupinus lepidus*, *Saxifraga bronchialis*, and *Penstemon davidsonii* var. *menziesii*) are also adapted to adverse summer conditions. Soil temperatures and soil moisture stress are high and possibly might exclude other plants even though they may be able to endure winter conditions.

Observations showed that phenological phases are closely related to time of snowmelt and early season temperature regimes. The ability of *Claytonia lanceolata* to flower within several days after snowmelt and complete its life cycle just before the vegetative canopy closes, at the base of the slope, is due in large part to its ability to initiate growth beneath the snow during fall or winter. Douglas and Taylor (1972), also working on Grouse Ridge, found *C. lanceolata* relatively well developed and in bud under 2 m of snow. Kimball *et al.* (1972) found new apical growth in early fall in Rocky Mountain populations of *C. lanceolata*. Other workers have also noted the ability of this and other alpine species to initiate growth at near freezing temperatures beneath snow (Billings and Bliss, 1959; Mooney and Billings, 1961; Halleck and Wiens, 1966;

Spomer and Salisbury, 1968). The fellfield species also show early phenological development enabling them to complete much of their seasonal growth before conditions become unfavorable.

Distribution of major alpine community types in western
North America

The numerous floristic works dealing with various regions of North America document the geographic range of most alpine vascular plant taxa adequately. An exception to this has been our knowledge of the North Cascadian flora. Recent collections have resulted in significantly new range extensions for 20 alpine species in western North America (Douglas and Taylor, 1970; Douglas *et al.*, 1973; Taylor *et al.*, 1973). The total known vascular flora for the alpine zone of the North Cascades consists of 250 species of which 165 occurred within the sampled stands.

This alpine flora appears to be much richer than that reported in alpine areas of Montana where Bamberg and Major (1968) report 120 to 185 species from three regions and Johnson and Billings (1962) report 191 from the Beartooth Plateau. Johnson (1970) recorded 129 species farther south in the San Juan Mountains of Colorado. The richer North Cascadian alpine flora may be due, in part, to the greater climatic diversity in the region and to the close proximity of these mountains to other ranges, both east and west as well as north and south.

The alpine flora of the North Cascades has floristic

affinities with many regions. The strongest affinities are with the arctic and cordilleran regions to the north and east. A smaller segment of the flora is restricted to the Pacific Coast, ranging from British Columbia to northern California. The Cascadian endemic element that ranges into the North Cascades consists of only a few species.

In contrast to our knowledge of plant ranges, information on the abundance of a taxa in a particular region is conspicuously poor. A number of papers, although describing the general vegetation of various regions, usually fail to document the relative abundance of the taxa thus making it difficult to recognize vegetation types for comparative purposes. The following discussion is based on the few studies that do allow comparisons with the North Cascadian communities. Future work will surely increase the geographic ranges of the communities presented here.

The ranges of the alpine plant communities are not necessarily restricted to the alpine zone. A number of them have subalpine-alpine distributions both in the North Cascades (Table 9) and elsewhere. Table 9 lends support for the inclusion of krummholz within the alpine zone, at least in the North Cascades, since more of the communities and a larger segment of the flora associated with krummholz occur in the alpine tundra above.

A number of community types may be restricted to the North Cascades. These include the *Calamagrostis purpurascens*,

TABLE 9. Numbers of alpine plant communities associated with the three vegetation belts or bands at upper elevations in the North Cascades Range.

Vegetation belts or bands	Region			
	Western North Cascades	Central North Cascades	Eastern North Cascades	Entire North Cascades
Alpine tundra	0	2	6	6
Alpine tundra- krummholz	5	6	5	6
Alpine tundra- krummholz-tree clump/meadow	6	7	4	10
Krummholz-tree clump/meadow	1	1	0	1
Total	12	16	15	23

Eriogonum pyrolaefolium-*Luzula wahlenbergii*, *Danthonia intermedia*, *Carex breweri*, and *C. capitata* types.

Of the snowbed communities the *Carex nigricans* type appears to be the most widespread. It occurs in both the subalpine and alpine zones in the Cascades of Oregon (Van Vechten, 1960) and central Washington (Meredith, 1972), the Olympic Mountains of Washington (Bliss, 1969; Kuramoto and Bliss, 1970), southern British Columbia (Archer, 1963; Brooke *et al.*, 1970; Eady, 1971), north to southern Alaska (Cooper, 1942), and east to the Canadian Rockies (Beder, 1967; Hrapko, 1970). The *Antennaria lanata* community, which also occurs in the subalpine zone of the eastern Cascades, is found in the Olympics (Bliss, 1969) and the Canadian Rockies (Beder, 1967; Hrapko, 1970). The *Eriogonum pyrolaefolium*-*Luzula wahlenbergii* community may be restricted to the North Cascades although similar, but drier, communities dominated by *Eriogonum pyrolaefolium* (but lacking *Luzula*) have been reported from Oregon (Van Vechten, 1960). The *Saxifraga tolmiei*-*Luzula wahlenbergii* type occurs only in the subalpine and alpine zones of the North Cascades and the nearby Coast Range of British Columbia (McAvoy, 1931; Brooke *et al.*, 1970).

Lush herb communities dominated by *Festuca viridula* and *Lupinus latifolius* are found in the subalpine and alpine zones in, and south of, the North Cascades. *Festuca viridula*-*Lupinus latifolius* (Franklin and Dyrness, 1969; Franklin *et al.*, 1971) and *Lupinus latifolius* (Meredith,

1972) types have been reported on Mount Rainier, Washington. These types have also been documented in the Three Sisters (Van Vechten, 1960) and Mt. Jefferson (Swedberg, 1961) areas in Oregon. Farther east, in the Wallow Mountains, Strickler (1961) has studied communities dominated by *Festuca viridula*. A similar *Festuca* (*F. idahoensis*) type occurs in the subalpine zone of the Olympic Mountains (Kuramoto and Bliss, 1970).

Several of the North Cascadian shrub types have wide geographic ranges. *Dryas octopetala*, a circumpolar species, occurs as a major dominant north to Alaska and the Yukon (Hansen, 1951; Price, 1971), east to the Rocky Mountains of Alberta (Beder, 1967; Bryant and Scheinberg, 1970; Hrapko, 1970) and south in the Rockies to Colorado (Johnson and Billings, 1962; Holoway and Ward, 1965; Marr, 1967; Bamberg and Major, 1968). The several heath types are also widely distributed in both the subalpine and alpine zones. They occur in the Olympics (Kuramoto and Bliss, 1970), the Cascades of Oregon (Van Vechten, 1960) and central Washington (Franklin *et al.*, 1971; Meredith, 1972), north to northern British Columbia (McAvoy, 1931; Archer, 1963; Brooke *et al.*, 1970; Eady, 1971; Welsh and Rigby, 1971) and the southwestern Yukon (Douglas, unpublished), and in the Rocky Mountains of Alberta (Heusser, 1956; Beder, 1967; Hrapko, 1970) and Montana (Bamberg and Major, 1968). *Cassiope tetragona*, found mainly in small clumps and mainly on north aspects in the eastern North Cascades, becomes a recognizable

type farther north (northwestern British Columbia and the southwestern Yukon) and east (Rocky Mountains of Alberta) (Hrapko, 1970; Welsh and Rigby, 1971; Douglas, unpublished). *Empetrum nigrum*, a circumpolar species, occurs as a community type in Alberta, the southwestern Yukon, and northern Alaska (Bliss, 1956; Hrapko, 1970; Douglas, unpublished). The circumpolar species, *Salix reticulata* has been reported elsewhere as a major dominant only from the southwestern Yukon (Price, 1971) and western Montana (Bamberg and Major, 1968). The *Salix cascadiensis* community is also rare in the literature, being documented only from Wyoming (Billings and Bliss, 1959). The *Arctostaphylos uva-ursi* type has been reported from western Montana by Bamberg and Major (1968).

Kobresia myosuroides, a wide ranging circumpolar species, has been reported as a dominant in many regions. This type has been described from Colorado to Alberta in the Rocky Mountains (Cox, 1933; Marr, 1967; Bamberg and Major, 1968; Hrapko, 1970; Bell, 1973) and north to the Kluane Ranges of the southwestern Yukon (Douglas, unpublished) and Mt. McKinley in Alaska (Hanson, 1951). It also occurs in the Sierra Nevada Mountains of California where it is a disjunct species (Major and Bamberg, 1963). Reports of other North Cascadian sedge types are sparse. *Carex scirpoidea* var. *pseudoscirpoidea* stands have been recorded in the Snowy Mountains of central Montana (Bamberg and Major, 1968) and the Sierra Nevada Mountains in

California (Major and Bamberg, 1963). *Carex nardina* is reported as a dominant in southwestern Alberta (Bryant and Scheinberg, 1970). The *Carex spectabilis* community appears to be mainly restricted to the subalpine and alpine zones of northwestern Washington and southern British Columbia (Kuramoto and Bliss, 1970; Eady, 1971; Douglas, 1972) although it also occurs as a snowpatch community in the Sierra Nevada Mountains (J. Major, personal communication).

In general, the communities restricted to the western or central North Cascades have closer affinities to coastal areas both to the north and south. Those communities restricted to the eastern North Cascades show closer affinities to Rocky Mountain and far northern areas.

The large number of community types recognized in the North Cascades Range is probably due, in large part, to the marked differences in climate across the range. Few other studies, at least in western North America, have included such a large geographic area or such a wide macroclimatic range, thus comparisons with other mountain regions is difficult.

SUMMARY

1. Alpine plant communities of the North Cascades Range, Washington and British Columbia were studied on 39 mountains in an area encompassing about 18,000 km².
2. The climate varies from maritime on the western slopes to more continental on the eastern slopes. This change in

macroclimate has a profound affect on regional vegetation patterns.

3. Twenty-three major community types were described from 128 stands. These included six snowbed types (*Saxifraga tolmiei*-*Luzula wahlenbergii*, *Eriogonum pyrolaeifolium*-*Luzula wahlenbergii*, *Carex nigricans*, *Antennaria lanata*, *Carex breweri*, and *Carex capitata*), two lush herb types (*Lupinus latifolius* and *Festuca viridula*), eight dwarf shrub types (*Cassiope mertensiana*, *Phyllodoce empetriformis*, *Phyllodoce glanduliflora*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, *Salix reticulata*, *Salix cascadiensis*, and *Dryas octopetala*), two dry grass types (*Danthonia intermedia* and *Calamagrostis purpurascens*), and five dry sedge types (*Carex spectabilis*, *Carex phaeocephala*, *Carex scirpoidea* var. *pseudoscirpoidea*, *Carex nardina*, and *Kobresia myosuroides*). Thirty-nine blockfield stands and 42 krummholz stands were also examined.

4. Soils in the region include poorly developed Entisols, weakly developed Inceptisols, and better developed Spodosols. The latter two soil types have developed in parent materials containing a high pyroclastic component. Physical properties are quite similar in most soils. Organic matter, total exchange capacity, and pH usually decrease from west to east. Exchangeable cations and nutrient levels are generally low throughout the region.

5. Alpha diversity measurements were applied to the 208 sampled stands. These measurements included species richness

or number of species (S), general diversity or richness and dominance concentration (\bar{H}), and equitability or evenness (E). In the mildest habitats (snowbeds and moist lower slopes) S , \bar{H} , and E were low due to dominance, through competition, by a few species. All measurements increased with increasing environmental rigor; a reflection of greater habitat heterogeneity. In the harshest habitats (upper ridges and blockfields), where physical factors render the habitat homogeneous (and relatively inhospitable), S and \bar{H} once again decline.

6. A fellfield-dry grass-lush herb environment gradient, 65 m in length, was examined on Grouse Ridge, Mt. Baker. High soil temperature and low soil moisture regimes were typical of the ridgetop fellfield while more moderate regimes occurred downslope. Soil temperatures decreased slightly, while soil moisture stress increased, with distance down the vegetated portion of the slope during drought periods. This is due to higher plant cover and greater evapotranspiration towards the base of the slope. Measurements of leaf ψ showed increases with distance downslope. Species exhibiting vigorous growth and high leaf ψ at the base of the slope had reduced vigor and much lower leaf ψ farther upslope. Phenological patterns were closely related to time of snowmelt and early season temperature regimes along the gradient.

7. The ranges of alpine plant communities in western North America are poorly documented. Several of the community

types appear restricted to the North Cascades Range, or the nearby Olympic Mountains of Washington or the Coast Range of southern British Columbia. A few of the types range south along the Cascade Range of central Oregon. Most of the community types range east to the Rocky Mountains and north to southern Alaska and the southern Yukon.

LITERATURE CITED

- Archer, A.C. 1963. Some synecological problems in the alpine zone in Garabaldi Park. M.S. Thesis. Univ. British Columbia, Vancouver, B.C. 129 p.
- Arno, F., and J.R. Habeck. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecol. Monogr. 42:417-450.
- Auclair, A.N., and F.G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes Area. Amer. Natur. 105:499-528.
- Ballard, T.M. 1972. Subalpine soil temperature regimes in southwestern British Columbia. Arct. Alp. Res. 4: 147-166.
- Bamberg, S.A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecol. Monogr. 38:127-167.
- Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156-181.
- Beder, K. 1967. Ecology of the alpine vegetation of Snow Creek Valley, Banff National Park, Alberta. M.S. Thesis. Univ. Calgary, Calgary, Alta. 243 p.
- Bell, K.L. 1973. Autecology of *Kobresia myosuroides*: why winter snow accumulation patterns affect local distribution. Ph.D. Thesis. Univ. Alberta, Edmonton, Alberta. 173 p.
- Bengsten, K.B. 1956. Activity of the Coleman Glacier, Mt. Baker, Washington, U.S.A., 1949-1955. J. Glaciol. 2:708-713.
- Billings, W.D., and L.C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology 40:388-397.
- Bliss, L.C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. 26:303-337.
- Bliss, L.C. 1962. Adaptations of arctic and alpine plants to environmental conditions. Arctic 15:117-144.
- Bliss, L.C. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44:678-697.

- Bliss, L.C. 1966. Plant productivity in alpine micro-environments on Mount Washington, New Hampshire. *Ecol. Monogr.* 36:125-155.
- Bliss, L.C. 1969. Alpine community patterns in relation to environmental parameters, p. 167-184. *In* K.N.H. Greenridge (ed.) *Essays in plant geography and ecology.* Nova Scotia Museum, Halifax, Nova Scotia.
- Bliss, L.C., and G.M. Woodwell. 1965. An alpine podzol on Mount Katahdin, Maine. *Soil Sci.* 100:274-279.
- Bockheim, J.G. 1972. Effects of alpine and subalpine vegetation on soil development, Mount Baker, Washington. Ph.D. Thesis. Univ. Washington, Seattle, Wash. 171 p.
- Bouyoucos, G.J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soil. *Agron. J.* 43:434-438.
- Boyer, J.S. 1967. Leaf water potentials measured with a pressure chamber. *Plant Physiol.* 42:131-137.
- Bray, J.R., and J.T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325-349.
- Brink, V.C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. *Ecology* 40:10-16.
- Brooke, R.C., E.B. Peterson, and V.J. Krajina. 1970. The subalpine mountain hemlock zone, p. 147-349. *In* V.J. Krajina and R.C. Brooke (eds.) *Ecology of western North America.* Vol. 2. Dept. of Botany, Univ. British Columbia, Vancouver, B.C.
- Bryant, J.R., and E. Scheinberg. 1970. Vegetation and frost activity in an alpine fellfield on the summit of Plateau Mountain, Alberta. *Can. J. Bot.* 48:751-772.
- Cain, S.A. 1938. The species-area curve. *Amer. Midland Natur.* 17:725-740.
- Coleman, E.A., and T.M. Hendrix. 1949. The fibreglass electrical soil-moisture instrument. *Soil Sci.* 67:425-438.
- Coombs, H.A. 1939. Mt. Baker, a Cascade volcano. *Geol. Soc. Amer. Bull.* 50:1493-1510.
- Cooper, W.S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. *Ecol. Monogr.* 12:1-22.

- Cox, C.F. 1933. Alpine plant succession on James Peak, Colorado. *Ecol. Monogr.* 3:299-372.
- Crandell, D.R. 1965. The glacial history of western Washington and Oregon, p. 341-353. In H.E. Wright, Jr. and D.G. Frey (eds.) *The Quaternary of the United States*. Princeton Univ. Press, Princeton, New Jersey.
- Crandell, D.R., D.R. Mullineaux, R.D. Miller, and M. Rubin. 1962. Pyroclastic deposits of Recent age at Mount Rainier, Washington. *U.S. Geol. Surv. Prof. Pap.* 450-D. 64 p.
- Daubenmire, R.F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Sci.* 33:43-66.
- Daubenmire, R. 1968. *Plant communities*. Harper and Row, New York. 300 p.
- del Moral, R. 1972. Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. *Bull. Torrey Bot. Club* 99:57-64.
- del Moral, R. 1973. The vegetation of Findley Lake Basin. *Amer. Midl. Natur.* 89:26-40.
- Douglas, G.W. 1971. The alpine-subalpine flora of the North Cascade Range, Washington. *Wasmann J. Biol.* 29:129-168.
- Douglas, G.W. 1972. Subalpine plant communities of the western North Cascades, Washington. *Arct. Alp. Res.* 4:147-166.
- Douglas, G.W., and T.M. Ballard. 1971. Effects of fire on alpine plant communities in the North Cascades, Washington. *Ecology* 52:1058-1064.
- Douglas, G.W., D.B. Naas, and R.W. Naas. 1973. New plant records and ranges for Washington. *Northwest Sci.* 47:105-108.
- Douglas, G.W., and R.J. Taylor. 1970. Contributions to the flora of Washington. *Rhodora* 72:496-501.
- Douglas, G.W., and R.J. Taylor. 1972. The biosystematics, chemotaxonomy, and ecology of *Claytonia lanceolata* Pursh in western Washington. *Can. J. Bot.* 50:2177-2187.
- Doughty, J.L. 1941. The advantages of a soil paste for routine pH determinations. *Soil Sci.* 22:135-138.
- Eady, K. 1971. Ecology of the alpine and timberline vegetation of Big White Mountains, British Columbia.

- Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 239 p.
- Embleton, C., and C.A.M. King. 1971. Glacial and periglacial geomorphology. Macmillan Co., Toronto, Canada. 608 p.
- Fonda, R.W., and L.C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecol. Monogr. 39:271-301.
- Ford, A.B. 1959. Geology and petrology of the Glacier Peak Quadrangle, northern Cascades, Washington. Ph.D. Thesis. Univ. Washington, Seattle, Wash. 337 p.
- Franklin, J.F., and C.T. Dryness. 1969. Vegetation of Oregon and Washington. U.S. For. Serv. Res. Pap. PNW-80. 216 p.
- Franklin, J.F., W.H. Moir, G.W. Douglas, and C. Wiburg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arct. Alp. Res. 3:215-224.
- Fryxell, R. 1965. Mazama and Glacier Peak ash layers; relative ages. Science 147:1288-1290.
- Gauch, H.G., Jr., and R.H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53:868-875.
- Goff, F.G., and P.H. Zedler. 1968. Structural gradient analysis of upland forests in the western Great Lakes area. Ecol. Monogr. 38:65-86.
- Hale, M.E., Jr., and W.L. Culberson. 1970. A fourth checklist of the lichens of the continental United States and Canada. Bryologist 73:499-543.
- Halleck, D.K., and D. Wiens. 1966. Taxonomic status of *Claytonia rosea* and *C. lanceolata* (Portulacaceae). Ann. Mo. Bot. Gard. 53:205-212.
- Hanson, H.C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. Ecol. Monogr. 21:317-378.
- Heusser, C.J. 1956. Postglacial environments in the Canadian Rocky Mountains. Ecol. Monogr. 26:263-302.
- Hickman, J.C. 1970. Seasonal course of xylem sap tension. Ecology 51:1052-1056.
- Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle, Wash. 730 p.

- Holway, J.G., and R.T. Ward. 1965. Phenology of alpine plants in northern Colorado. *Ecology* 46:73-83.
- Hrapko, J.O. 1970. An ecological study of the alpine plant communities on Signal Mountain, Jasper National Park. M.S. Thesis. Univ. Alberta, Edmonton, Alta. 283 p.
- Jenny, H. 1941. Factors of soil formation. McGraw-Hill, New York. 281 p.
- Johnson, K.L. 1970. Alpine vegetation and soils of Mesa Seco Plateau, San Juan Mountains, Colorado. Ph.D. Thesis. Univ. Illinois, Urbana, Ill. 217 p.
- Johnson, P.L., and W.D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol. Monogr.* 32:105-135.
- Kimball, S.L., B.D. Bennett, and F.B. Salisbury. 1973. The growth and development of montane species at near-freezing temperatures. *Ecology* 54:168-173.
- Klikoff, L.G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. *Ecol. Monogr.* 35:187-211.
- Kruckeberg, A.R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* 35:267-274.
- Kruckeberg, A.R. 1969. Plant life on serpentinite and other ferromagnesian rocks in northwestern North America. *Syesis* 2:15-114.
- Kulczński, S. 1937. Zespoly roslin w Pieninach - Die Pflanzenassoziationen der Pieninen. *Polon. Acad. des Sci. et Lettres, Cl. des Sci. Math. et Nat. Bull. Int. ser B (Suppl. II)* 57:203.
- Kuramoto, R.T., and L.C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. *Ecol. Monogr.* 40:317-347.
- Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan. 362 p.
- Löve, A., D. Löve, and B.M. Kapoor. 1971. Cytotaxonomy of a century of Rocky Mountain orophytes. *Arct. Alp. Res.* 3:139-166.
- Lowery, R.F. 1972. Ecology of subalpine zone tree clumps

- in the North Cascade Mountains of Washington. Ph.D. Thesis. Univ. Washington, Seattle, Wash. 137 p.
- Major, J. 1951. A functional, factorial approach to plant ecology. *Ecology* 32:392-412.
- Major, J., and S.A. Bamberg. 1963. Some Cordilleran plant species new for the Sierra Nevada of California. *Madrono* 17:93-109.
- Marr, J.W. 1967. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colorado Stud. Ser. Biol. No. 8. 134 p.
- McAvoy, B. 1931. Ecological survey of the Bella Coola region. *Bot. Gaz.* 92:141-171.
- McLean, A. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationships to soils. *Ecol. Monogr.* 40:403-424.
- Meredith, D.H. 1972. Subalpine cover associations of *Eutamias amoenus* and *Eutamias townsendii* in the Washington Cascades. *Amer. Midl. Natur.* 88:348-357.
- Misch, P. 1952. Geology of the northern Cascades of Washington. *Mountaineer* 45:4-22.
- Misch, P. 1966. Tectonic evolution of the northern Cascades of Washington State. *Can. Inst. Mining and Metallurgy Spec.* Vol. 8:101-148.
- Mooney, H.A., G.S. Andre, and R.D. Wright. 1962. Alpine and subalpine vegetative patterns in the White Mountains of California. *Amer. Midl. Natur.* 68:257-273.
- Mooney, H.A., and W.D. Billings. 1961. Comparative physiological ecology of arctic and alpine populations of *Oxyria dygnia*. *Ecol. Monogr.* 31:1-29.
- Mulligan, G.A. 1970. Cytotaxonomic studies of *Draba glabella* and its close allies in Canada and Alaska. *Can. J. Bot.* 48:1431-1437.
- Mulligan, G.A. 1971. Cytotaxonomic studies of *Draba* species of Canada and Alaska: *D. ventosa*, *D. ruaxes*, and *D. paysonii*. *Can. J. Bot.* 49:1455-1460.
- Mullineaux, D.R. 1964. Extensive Recent pumice lapilli and ash layers from Mount St. Helens volcano, southern Washington. *Geol. Soc. Amer. Spec. Pap.* 76:285. (abstr.)
- Nasmith, H., H. Mathews, and G.E. Rouse. 1967. Bridge River ash and some other Recent ash beds in British

- Columbia. Can. J. Earth Sci. 4:163-170.
- Nimlos, T.J., and R.C. McConnell. 1965. Alpine soils in Montana. Soil Sci. 99:310-321.
- Nimlos, T.J., R.C. McConnell, and D.L. Pattie. 1965. Soil temperature and moisture regimes in Montana alpine soils. Northwest Sci. 39:129-138.
- Peterson, S.M. 1971. Microenvironment and water relations of two alpine species, Olympic National Park. M.S. Thesis. Univ. Alberta, Edmonton, Alberta. 63 p.
- Pielou, E.C. 1967. The use of information theory in the study of diversity of biological populations. Proc. 5th Berkeley Symp. Math. Statist. Probab. 4:163-177.
- Porter, S.C., and G.H. Denton. 1967. Chronology of neoglaciation in the North American Cordillera. Amer. J. Sci. 265:177-210.
- Powers, H.A., and R.E. Wilcox. 1964. Volcanic ash from Mount Mazama (Crater Lake) and from Glacier Peak. Science 144:1334-1336.
- Pritchard, N.M., and A.J.B. Anderson. 1971. Observations on the use of cluster analysis in botany with an ecological example. J. Ecol. 59:727-747.
- Price, L.W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. Ecology 52:638-647.
- Rubin, M., and C. Alexander. 1960. U.S. Geological Survey radiocarbon dates V. Amer. J. Sci. Radiocarbon Suppl. 2:129-185.
- Schofield, W.B. 1968. A checklist of Hepaticae and Anthocerotae of British Columbia. Syesis 1:157-162.
- Schofield, W.B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. Madrono 20:155-207.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339-346.
- Scholander, P.F., H.T. Hammel, E.A. Hemmingsen, and E.D. Bradstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Nat. Acad. Sci. 52:119-125.
- Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana. 125 p.

- Slatyer, R.O. 1967. Plant-water relationships. Academic Press, New York. 366 p.
- Soil Survey Staff. 1970. Selected chapters from the unedited text of the soil taxonomy of the National Cooperative Survey. U.S. Dept. Agric., Soil Conserv. Service, Soil Survey, Washington D.C., December, 1970.
- Spomer, G.G., and F.B. Salisbury. 1968. Eco-physiology of *Geum turbinatum* and implications concerning alpine environments. Bot. Gaz. 129:33-49.
- Strickler, G.S. 1961. Vegetation and soil condition changes on a subalpine grassland in eastern Oreg U.S. D.A. For. Serv. Pacific Northwest For. Range Exp. Sta. Res. Pap. 40. 46 p.
- Swedburg, K.C. 1961. The coniferous ecotone of the east slopes of the northern Oregon Cascades. Ph.D. Thesis. Oregon St. Univ., Corvallis, Oreg. 118 p.
- Taylor, R.J., G.W. Douglas, and L.M. Sundquist. 1973. Contributions to the flora of Washington. II. Northwest Sci. 47:169-179.
- U.S. Weather Bureau. (no dates). Station climatic records for Mt. Baker.
- van der Valk, A.G., and L.C. Bliss. 1971. Hydrarch succession and net primary production of oxboy lakes in central Alberta. Can. J. Bot. 49:1177-1200.
- van Ryswyk, A.L. 1969. Forest and alpine soils of south-central British Columbia. Ph.D. Thesis. Washington St. Univ., Pullman, Wash. 178 p.
- Van Vechten, G. 1960. The ecology of the timberline and alpine vegetation of the Three Sisters, Oregon. Ph.D. Thesis. Oregon St. Univ., Corvallis, Oreg. 111 p.
- Walkley, A., and T.A. Black. 1934. An examination of the Dectjareff method for determining soil organic matter and a porposed modification of the chronic acid titration method. Soil Sci. 37:29-38.
- Washburn, A.L. 1956. Classification of patterned ground and review of suggested origins. Bull. Geol. Soc. Amer. 67:823-865.
- Welsh, S.L., and J.K. Rigby. 1971. Botanical and physiographic reconnaissance of northern British Columbia. Brigham Young Univ. Sci. Bull. Biol. Ser. 15. 49 p.
- Westgate, J.A., and A. Dreimanis. 1967. Volcanic ash

layers of Recent age at Banff National Park, Alberta, Canada. Can. J. Earth Sci. 4:155-161.

Westgate, J.A., D.G.W. Smith, and H. Nichols. 1969. Late Quaternary pyroclastic layers in the Edmonton area, Alberta, p. 179-186. In S. Pawluk (ed.) Pedology and Quaternary research. Univ. Alberta, Edmonton, Alta.

Whittaker, R.H. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. Ecology 35:275-288.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279-388.

Whittaker, R.H. 1970. Communities and ecosystems. Mcmillan Co., New York. 158 p.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

Wilcox, R.E. 1965. Volcanic-ash chronology, p. 807-816. In H.E. Wright, Jr. and D.G. Frey (eds.) The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Young, S.B. 1970. On the taxonomy and distribution of *Vaccinium uliginosum*. Rhodora 72:439-459.

B30072